NOMOGENESIS

OR

EVOLUTION DETERMINED BY LAW

BY

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WITH AN INTRODUCTION BY

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TRANSLATED FROM THE RUSSIAN
BY
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res quaeque suo ritu procedit, et omnes
foedere naturae certo discrimina servant.

LUCRETIUS, *De rerum natura*, V. 923-924.

Nach ewigen ehrnen
Grossen Gesetzen
Mussen wir alle
Unseres Daseins
Kreise vollenden.

GOETHE.

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TO

THE MEMORY OF HIS FATHER

SIMON BERG

(1844-1898)

THIS BOOK IS REVERENTLY DEDICATED

BY THE AUTHOR

Laus illi debetur et a me gratia major.

Science commits suicide when she adopts a creed.

HUXLEY.

INTRODUCTION

Professor L. S. Berg is an accomplished zoologist, an experienced traveller, a learned and a thoughtful man. He speaks from the old standpoint of the Naturalist, the broad platform from which Darwin and Wallace, Hooker and Huxley, looked out upon the world; and he writes his book to help us explore the orderly sequence, or (if we please to put it so) the underlying laws, of what once seemed to be the accidents of Variation and the chance-medley of the course of Evolution.

Some forty years ago, speaking to an Oxford meeting of the British Association on some of the "difficulties of Darwinism," I used the phrase "laws of growth" in very much the same sense (though with a stronger leaning to the physical side) as Dr. Berg means by his word "Nomogenesis." My old master Professor Alfred Newton was in the chair, and (good friend to me though he always was) he did not hide his impatience and disapproval; there were *no* difficulties in Darwinism, either to him or any other sensible man in those days. New developments might haply come, such as Bates and Fritz Müller had brought in; but they would assuredly be found to fit neatly and firmly, just as these had done, within the four corners of the fabric. The scientific world was convinced by the logic and content with the simplicity of the Darwinian concept, and its convictions were on no account to be disturbed.

Since those days many things have happened, and Bateson has come—and, alas, has gone. It was Bateson, far more

than any other, who showed us that there *were* difficulties in Darwinism, that the problems of Evolution were far from settled, that the origin of species was, in fact, an unsolved mystery. His study of Variation shattered the "crude belief" that Natural Selection had, of itself, impressed form and symmetry on the organic world. He brought Mendel back from his grave, and showed us that when the old Abbot counted his peas in their pods he made one of the greatest and most pregnant of all experimental discoveries, and that wellnigh the whole subject of heredity hangs thereby. Not the least of his great services was to keep a balanced mind through all the modern welter of experiment and hypothesis. and to remind us that though our knowledge increased our ignorance was scarcely diminished.

Facts accumulate and the rare touch of genius illuminates them now and then; but all the while there is another way by which knowledge grows and wisdom comes. The world does a deal of quiet thinking; it comes slowly to sound conclusions, and from its considered judgments there is no appeal; long discussion and consideration by plain ordinary folk, by the rank and file of educated men, winnow all our theories and divide the false from the true. We know that Evolution takes place, the whole world says so; a few wise men knew it long ago, and so might we have done had our heads not been full of another story told us with matchless skill. But apart from the cardinal fact itself, I doubt whether there is another aspect of the case on which the world has yet made up its mind; for many a day to come we must continue to ponder and discuss the *modus operandi* of evolution, refer the case again and again *ad avizandum* (as the Scotch lawyers say), and postpone our final judgment.

Books like Dr. Berg's are a help and a stimulus to such long and necessary discussion. Dr. Berg does not beat about the bush; he is intensely controversial, but he is modest withal; we may agree with him or not, just as we please; he says what he thinks in plain candid words, and he raises an

issue on every page. He has made up his mind that the Origin of Species does not come about " by means of Natural Selection." Species come into being, so he says, much as individuals do, and they perish in like manner when their day is done ; neither their coming nor their going is due to the " vagaries of chance," but the whole process is an orderly one, defined by strict natural law. When we come to search for these laws we discover our ignorance. Mendel's law we know, but no other so general or so trustworthy ; we are fain to eke out our scanty knowledge by invoking principles which we think we recognise, and by using phrases which we can only partly explain ; how species are actually produced remains an unsolved riddle, it is a great mystery. Here at least is a conclusion which few men of our time will venture to dispute.

Dr. Berg maintains stoutly that environment, or what he calls the " geographical landscape," has its direct effect on flora and fauna. That bird and beast and creeping thing tend, for instance, to take on the sandy hue of the surrounding desert is a phenomenon not to be accounted for by selection ; a common principle is at work, and its effects are seen throughout an entire population. Tundra, forest, steppe and desert, mountain and cavern, island, lake and sea, each stamps its mark on its inhabitants ; life is coupled with a "principle of regulation" reacting to all the circumstances of the case, and thereby it adapts itself to such conditions or such habitations as these.

There are cases where evolution would seem to set a certain course with no particular object, and to be reluctant to turn back ; the course once laid down is followed far, and sometimes it runs along strange lines of transformation. In the Orchid flower, for example, it seems impossible to assert that usefulness is at the root of the matter ; each little singularity, whatsoever it may be, is gradually enhanced, and persistent exaggeration would seem to be the only motive of the shapes assumed. There is some-

thing here which we do not comprehend, and cannot explain; and our author is fain to borrow from an older philosophy, as Goebel and other botanists have already done, the postulate of a "formative principle" or "Gestaltungstrieb."

No place is left for Chance in the manifestation of new characters; the course of evolution is fixed and determined. The same laws are at work in the growth of the individual as operated with like results in former generations; and what we call "recapitulation" means nothing more. We are apt to be perplexed or deceived in countless cases by similarity of unrelated organs, or by "convergent resemblance" of unrelated organisms. The working of identical laws is enough to account for such similarities, and so-called Mimicry is but a particular case of the convergent resemblance to which it leads.

I need go no further, nor say one word more, to show that Professor Berg holds views of his own, with many of which many of us are little likely to agree. But his book is always interesting; and he himself is so modest, so candid, so careless of credit and priority, that we may differ from him and still be friends. He tells us mueh of recent Russian work, of which we know all too little and of some of which we might not otherwise have heard; and this adds in no small measure to the value of the book. Russian seience is a very great thing; we could ill do without it, we were the poorer when it was eclipsed, we rejoice in its vigorous resuscitation. I for one am grateful to Professor Berg for his original and suggestive book.

D'Arcy Wentworth Thompson.

PREFACE

THE object of the following pages is to show that the evolution of organisms is the result of certain processes inherent in them, which are based upon law. Evolution is *Nomogenesis*, development in accordance with definite laws, and not, as was believed by Darwin, development due to chance. In this process the struggle for existence and natural selection possess but secondary importance, and progress in organisation in no degree depends on the struggle for existence.

The conclusions presented in this book have been reached by me quite independently, and have been drawn from my studies on the taxonomy and geographical distribution of fishes. It in nowise follows, of course, that all which is offered here is new. Many of the arguments set forth by me have been earlier submitted by other writers. But questions of priority interest me least of all in this case, and even if it happens that all my arguments have already been advanced by others, I renounce once for all any claims that I may have to "priority."

Darwin's theory served its useful purpose by giving a powerful impetus to scientific thought and thereby inciting to further investigation. But in questions of evolution a further advance is at present feasible only if we lay aside the erroneous assumption that the struggle for existence and selection are factors of progress. Even error, if it be acknowledged as such, may lead to progress; so says a distinguished adherent of the theory of selection, Plate,

in reference to another matter. The same idea was expressed in other words by Herbert Spencer, who said that mankind can follow a straight course after having exhausted all possible crooked ways.

I would remind those who may feel indignant at the "heretical" opinions set forth in these pages, that science should be averse to dogmatism and to a blind reverence to authority. There is no doctrine, not even excepting the laws of Newton, which is proof against criticism. It is, on the contrary, always salutary to hear opinions which do not conform with those generally held. "There is always hope when people are forced to listen to both sides," says J. S. Mill ("On Liberty"); "It is when they attend only to one that errors harden into prejudices, and truth itself ceases to have the effect of truth, by being exaggerated into falsehood."

In the present book no hypothesis is evolved: facts speak for themselves, and all hypotheses inconsistent with them, however precious they may seem to us, will have to give way before their force. "The chief duty of a scientist ought to consist, not in endeavouring to prove the infallibility of his opinions, but in being ever ready to reject an idea that cannot be proved, or an experiment that is unconvincing" (Berthelot). Facts, in my opinion, testify in favour of Nomogenesis, and not in favour of the hypothesis of chance.

It is as yet impossible to establish the general laws to which evolution is subject; neither was it the aim of the author to formulate such laws. And yet certain regularities may be observed to occur, which have been duly pointed out in the corresponding parts of the text.

It may not be out of place to mention that the author has invariably endeavoured to keep to the solid ground of Science without trespassing into the field of metaphysical hypotheses.

It remains for me to say that although in complete disagreement with Darwin's opinions as to the part played by the

struggle for existence, I none the less entertain feelings of the highest respect for the personality and the works of the great English naturalist. I may conclude with the following words of N. J. Danilevsky (i. p. 11), "Whoever has read and studied the works of Darwin can doubt anything, but not the deep sincerity and nobility of his mind." Both as a scientist and as a man Darwin stands on an unattainable height.

The Russian edition of this work appeared in 1922. Much new information based upon the most recent publications has been incorporated in the present English edition.

This book has been translated from Russian with much care by J. N. Rostovtsov, to whom I take this opportunity of expressing my most cordial thanks for the great labour expended on that work.

I tender my warmest thanks to Professor N. I. Vavilov for the kindness with which he has given me access to his private library, as well as to the library of the Bureau of Applied Botany, and for his most valuable assistance in the preparation of the English edition.

L. S. Berg.

Bureau of Applied Ichthyology,
Leningrad, *January*, 1924.

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CHAPTER I

THE STRUGGLE FOR EXISTENCE AND NATURAL SELECTION

However true, said Socrates, the first principles may appear to us, they should still be examined in the most careful manner.
PLATO, "Phaedo."

In judging of a matter that is not self-evident the wise should be governed by the principle of the greatest probability.
CICERO, "On the Nature of Gods," i, ch. v.

Any theory of evolution which omits the explanation of the causes of variations is faulty at the basis.
COPE, "The Primary Factors of Organic Evolution," 1896.

1. THE THEORIES OF THE ORIGIN OF ADAPTATIONS IN ORGANISMS

EVERY property of the organism that conduces to the prolongation of the life of the individual or of the species, we call purposive (fit), and such as contributes to the shortening of life, non-purposive (unfit).

Bodies that respond to stimuli in a purposive manner may be called living. To this it might be objected that such a definition rests on a vicious circle, life being defined by the conception of fitness, which itself is contributory to life. But, in effect, as may be seen from the following definition, no such vicious circle is present: a living body is a body which, as a rule, responds to stimuli in such a manner as to insure the subsequent existence of the given individual (or the species to which it belongs). To non-living bodies, in my opinion, no such property may be attributed without straining the point. In case further

doubts may arise on the subject, to this definition it might be added that *living matter is capable of systematically transforming heat into work* (we may here remind the reader that machines possessing the same capacity are the products of the human mind and hands). *Living bodies* may thus be defined *as responding, as a rule, to stimuli in a purposive manner and systematically transforming heat into work.* It would seem to us that by such a definition, embracing all the characters of the living body, the latter can always be *distinguished from a non-living body* (*i.e.* either one that had been, or one that had never been, alive).

J. Loeb (1906, p. 1), an extreme adherent of the mechanistic conception of vital phenomena, regards living beings as chemical machines consisting principally of colloidal substances and possessing the capacity of automatic development, self-preservation and reproduction. Nothing could be urged against this definition, beyond the observation that beings so defined may be termed "machines" in a metaphorical sense only, as no machine properly so called possesses any of the characters mentioned by Loeb: machines never consist of colloids, neither are they endowed with a capacity for automatic development, automatic self-preservation or automatic propagation.

The American physiologist further expresses a hope that in the future science will be able to construct a "living machine." On this point opinions may differ, but in any case we are entitled to base such an assumption on the one premise that the "living machine" will be constructed by another "living machine," *i.e.* man. For a strictly mechanistic conception of life can be held only on the assumption that the "living machine" be constructed by the unaided forces of inorganic nature alone. But such an assumption is no more justifiable than the expectation of finding in the state of nature a watch, or a steam-engine, or a volume of "War and Peace," composed by the blind agency of atoms without any intervention on the part of the human mind.

So far, at least, the principle of *omne vivum e vivo* alone holds the ground.

In order to be able to accomplish purposive acts the organism possesses adaptations. Every such adaptation presupposes (1) adequate structure, and (2) adequate function, or capacity to utilise a given organ.

It cannot be claimed that living matter always reacts in a purposive manner. For if this were so, it would mean that organisms had attained the greatest conceivable perfection. But such is by no means the case: numerous perversions of instincts, such as the flight of moths towards the fire, the extermination by the female of her progeny, sexual attraction towards members of the same sex, abortive regeneration, the phenomena of anaphylaxis,[1] clearly bear witness to the absence of a complete fitness in the animal's functions. We cannot, therefore, agree with the opinion of Peter (1920, pp. 40, 41), according to which organisms do not in general possess injurious organs or properties.

Yet, as a general rule, organisms, so far as it lies in their power, respond to stimuli in a purposive manner. An overwhelming majority of organs and plants are so constructed as to be ideally adapted to the proper exercise of their functions.

In ascertaining the mechanism by which these adaptations are formed, lies the problem of the Theory of Evolution. It is obvious that such characters of a living being as are not adaptive, or, in other words, are neutral in their relation to the life and death of the individual, arise (and this can scarcely be disputed) in a purely mechanical manner, in obedience to physical and chemical laws; furthermore, they arise without the intervention of chance. But a number of difficulties spring up when we endeavour to ascertain the origin of purposive characters or adaptations.

[1] Anaphylaxis signifies a state of hypersusceptibility, the reverse of immunity: on repeated injections of a given substance the organism not only fails to get used to the effects, but even reacts more energetically than after the first injection, sometimes succumbing after the introduction of extremely minute doses.

Speaking generally, none but the following solutions of this last problem are admissible.[1]

I. Fitness is the consequence of a fortuitously happy combination of circumstances. This conception, primarily due to Empedocles, Epicurus and Lucretius, has been fully elaborated by Darwin.[2]

The substance of the celebrated English naturalist's theory may be formulated in the following manner ("Origin of Species," chap. iv, p. 102; "Variation of Animals and Plants," 1868, v. i, pp. 5-6):—

(i) All organisms tend to increase so rapidly that the entire Earth's surface would not be large enough to hold the progeny of a single pair.

(ii) As a consequence, there ensues a perpetual struggle for existence, in which the strongest ultimately prevail and the weakest fail.

(iii) All organisms vary, however slightly, through the effects of changes in the environment, and other causes.

(iv) Throughout the course of ages hereditary variations may arise by chance. It may by chance occur that such hereditary variations can in some way become useful to those individuals which they affect. It would be surprising had beneficial variations never arisen; for it is notorious that domesticated animals and cultivated plants present many variations that have been taken advantage of by man for his own profit or pleasure.

[1] We shall henceforward consider those solutions alone which relate to *immanent* fitness, *i.e.* which is inherent in the object of purposive acts; in other words, in the organism itself. The father of the theory of immanent fitness is Aristotle. The adherents of *transcendental* fitness, on the contrary, seek the cause in a certain transcendental power by which an efficient order of the world has been established from the very beginning. We may illustrate the latter point of view by quoting the following words from the "Optics" of Newton, who was a believer in transcendental fitness—"The original structure of such exquisitely conceived parts of animals as eyes, ears, brain, muscles, heart, etc., as also the instinct of animals and insects, cannot be the creation of anything but the wisdom and genius of the mighty, ever-living Agent."

[2] The history of the subject has been fully set forth in my book, "The Theories of Evolution." Petrograd, 1922 (in Russian).

(v) If such chance variations occur (iv), those which are beneficial (in however slight a degree) will be preserved, while those which are injurious will disappear. An overwhelming majority of individuals will perish in the struggle for existence, and only a chosen few, in whom variations useful to the organism are exhibited, will have the chance of surviving. The survivors will, by means of heredity, transmit their more perfect organisation to their progeny.

(vi) This preservation in the struggle for existence of varieties possessing some advantageous features in structure, physiological properties or instinct, Darwin calls *natural selection*, and Spencer *the survival of the fittest*.

We have exposed Darwin's theory practically in his own words. His theory thus requires that,

(*a*) variations be so multifarious as to include among new characters such as by chance may be useful,

(*b*) that these useful characters be transmitted through heredity,

(*c*) that the surviving individuals should be distinguished by some useful characters from those which have perished, *i.e.* that mortality be not accidental, but, as it is usually designated, selective,

(*d*) that the number of individuals accidentally possessing useful characters and therefore surviving should be very small in comparison with those which have perished ; if the reverse were the case, development in a determined direction would be manifested.[1]

If these premises are founded on what actually occurs in Nature, the theory of natural selection may effectively explain not only the origin of purposive characters as being due to accidental usefulness, but likewise gradual perfection in organisation, or progress, as being the result of the survival of the fittest.

Whether this actually happens in Nature will be considered later.

[1] This latter point will be considered in a subsequent chapter.

II. The adherents of *vitalism* aver that fitness is the effect of the operation of a distinct vital force, which is manifest in organisms alone, and differs from the forces with which physics and chemistry deal.[1]

Let us quote the following words of one of the most renowned physicists of the nineteenth century, Hertz (1894, p. 45), the discoverer of electrical waves: "We cannot actually affirm that the inner processes of living beings are subject to the very same laws as those of inorganic nature, but neither can we assert that they are subject to other laws. But if we judge from external appearances and share the *commonly accepted views, we are obliged to admit* a radical distinction in this case. The very sentiment which compels us to exclude from the mechanics of inanimate nature every conception of aim, feeling, pleasure and pain, makes us hesitate to deprive the organic world of all this wealth of colour."

In these words the sentiments of a naturalist are forcibly expressed; but the history of science has taught us that vital force, as a hypothesis, is valueless: it has in nowise aided us in making any progress in the interpretation of facts. We are enabled to work fruitfully in the field of natural science only by the aid of forces recognised in physics, and every naturalist should as far as possible endeavour to interpret nature by mechanical means, as was insisted upon by Kant in his "Critique of Judgment" ("Kritik der Urteilskraft," 1790, § 77).

The theory of vitalism simply expresses the fact of the presence of purposive adaptations, but it leads us no further on the way towards their full comprehension. To the same class as vitalism may be referred Schopenhauer's doctrine of the will,[2] Hartmann's of the unconscious, Driesch's of

[1] In a Russian school text-book of physics by Lenz, which was much in vogue in the first half of the nineteenth century, we find the following: "It has been possible to refer all natural phenomena to the simplest agencies or forces; they are the following: gravitation, molecular attraction, chemical affinity, heat, electricity and *vital force.*"

[2] Schopenhauer, "Ueber den Willen in der Natur," p. 41: "nach dem Willen jedes Thiers hat sich sein Bau gerichtet."

entelechy, and Bergson's (1907) of vital impulse (*élan vital*).

III. Fit adaptation is the consequence of the power inherent in all organisms of acting with a definite purpose, whether throughout life or during a certain period of development. Such a view (animistic), having as its source the psychology of Aristotle and subsequently developed by Leibnitz, was in the course of time all but absorbed by vitalism. But its elements can still be found in Darwinism, namely in the conception of the struggle for existence, or to be more definite, in the natural struggle of organisms for food and reproduction, where the *will* emerges as the primary agent. This doctrine is further developed by Wundt (i, 1907, pp. 324-325) under the name of *voluntarism*: the activity of living beings, governed by the will, and chiefly concerned in the accomplishment of the possibilities of nutrition and reproduction, leaves traces in the organism in the shape of a certain predilection for repeating the same actions on the recurrence of similar conditions. The instincts of animals may serve as an illustration of the foregoing. Every habitual movement leaves permanent traces in the nervous system, and thus gradually transforms a voluntary act into a purely mechanical one. Every acquisition of a habit is a miniature of the history of the development of the organic world. The forces which give birth to purposive structures do not go beyond the organism, neither are they displayed as unconscious factors: they are the products of the work of the will.

IV. Purposive adaptation is one of the fundamental properties of the living being (not liable to further resolution into elements), such as irritability, contractility, capacity for nourishment, assimilation, reproduction. It is neither more, nor is it less, incomprehensible than any of the properties enumerated. A living being devoid of purposive structures would be inconceivable. To comprehend the origin of adaptations in the living being is to comprehend the essence

of life. And the essence of life is no easier to comprehend than the essence of matter, energy, feeling, consciousness and will.

Life, says Claude Bernard, is neither more, nor less, obscure than any of the other first principles (1878, p. 64). The same opinion is shared by Herbert Spencer (1898): "We must admit," *he says*, "that life in its essence cannot be conceived in physico-chemical terminology. . . . We must simply own that both in this, as in all other directions, our explanations in the end bring us face to face with the inexplicable: finite reality concealed beneath any given manifestation, as indeed beneath all manifestations, exceeds our understanding. It is enough to consider how unintelligible are even the simplest forms of existence in their finite nature, in order to perceive that life, that most complex form of existence, is doubly so."[1]

In other words, we here encounter a metaphysical problem, the solution of which it is equally permissible to seek in the direction followed by Wundt (see III, above).

Purposive structure and action are thus *a fundamental property of the living being*. This is the point of view I adopt.[2]

One of the consequences of the principle of aboriginal purposive adaptation, which we support here, is the doctrine of the effect of the use or disuse of organs, or Lamarckism. And, as a matter of fact, all authors, both those who fully share Lamarck's views, and those who admit Lamarck's principles as well as the theory of natural selection (as Darwin,[3]

[1] Herbert Spencer, "Principles of Biology," suppl. chap. vi to the edition of 1898.

[2] I have now learnt that the same opinion was reached before me by R. E. Lloyd (1914, p. 74).

[3] Thus Darwin in "The Origin of Species" (ch. v, pp. 108-112, Ed. 6) attributes the atrophy of wings in island birds and insects to the disuse of these organs, and the absence of eyes in many cave animals to the same cause. In chap. xv of the same work (p. 421, 1872), Darwin calls the use and disuse of organs important agencies in evolution. In chap. xxiv of "The Variation of Animals and Plants" (1868) the consequences of the use and disuse of organs are fully discussed (pp. 295-303). See also "Descent of Man," chap. ii.

Spencer, Plate and many others have done) unconsciously advocate the view that purposive adaptation is a fundamental property of the living being, not susceptible of further resolution into elements.

And, indeed, what else is meant by Lamarck's first law (1809, ch. vii) ?—" In every animal which has not reached the limits of its development, more frequent and continuous use of any organ *gradually strengthens, develops and increases it, and endows it with force proportionate to the length of time it was in use.* The continuous disuse of any organ, on the other hand, gradually weakens it, lets it fall into decay, progressively diminishes its capacity for work and finally leads to its extinction." [1]

This law signifies no more than the capacity of the organism to support and develop necessary organs and to dispense with useless ones, and such a capacity we call purposive behaviour.

It may be said that the use of an organ causes an inflow of blood and a consequent supply of nutrient matter, thus enabling it to be further developed and improved. But there still remains the problem,—why should a more vigorous exercise of the functions cause a more copious flow of blood to the organ ? For the latter is a purposive act, which itself requires explanation.

The use of any object belonging to the inorganic world generally causes its wear and tear, not its development and improvement. Every instrument wears out with use : a saw, a hatchet, or a pen becomes blunt ; from the effects of water and air granite disintegrates into gravel, and never becomes harder or more solid ; iron is transformed into rust, etc. Living beings alone are improved by use. Only when the organism ages and gradually prepares for transformation into the state of non-living matter, does the

[1] We may quote here one of Lamarck's examples : if, in order to satisfy its needs, an animal makes repeated efforts to lengthen its tongue, that organ will finally acquire a considerable length (ant-eater, green woodpecker).

continuous use of organs cause them to wear out: teeth may be offered as an example.

A good illustration of the foregoing is supplied by the considerations of Plate ("Selektionsprinzip," p. 209) as to the following very serious objection, which is raised against the theory of selection: "It is highly incredible that in the evolution of a complex organ the requisite variations should occur simultaneously and in a harmonious manner." Why, for instance, should the variations in the corolla of orchids correspond to the forms of the insects by which they are fertilised? Or why should modifications in the generative organs of the male correspond to those of the female? What causes such a coordination, and why should it occur in both simultaneously?

If, says Plate, we admit with Lamarck, Darwin, Spencer and Haeckel the principle of the inheritance of acquired characters, it would then be possible to answer thus the question submitted to us. Suppose we are asked to explain why in the giant deer,[1] along with the increase in the size of the antlers the bones of the skull become thicker, the nuchal muscles swell in volume, the fore-limbs become stronger. It might be explained in this wise. Let us assume that for some reason or other the antlers have grown in size and weight; the excitation produced in the frontal bones by this growth would cause a thickening of these bones; a more powerful stress on the nuchal ligament would be conveyed to the spinous processes of the vertebrae, and the musculature of the neck and fore-limbs would have to be more vigorously exerted under the weight of the antlers, and consequently would be more powerfully developed. All these modifications would be transmitted to posterity, and in this way a species of deer would arise, in which the size of the antlers would be coordinated with a series of other characters.

These arguments constitute a very typical example of

[1] or Irish "elk," *Megaceros giganteus*.

a case of *petitio principii*, and as such are worthy of being inserted in text-books of logic. For, indeed, we might ask, "Why should the muscles of the neck increase simultaneously with the size of the antlers?" To this question comes the answer "Because the increase in the size of the antlers had produced a stimulation of the organism and had compelled it to act in an expedient manner." But why should the stimulation have caused this effect? That is the very problem which still requires explanation, for an answer such as we have received really means nothing. Let us take an analogous example. Why does water attain its maximum density at a temperature of 4° C.? Because a fall (or increase) of temperature to 4° C. causes it to acquire that condition. Could any one regard this answer as an explanation?

Why should stimulation cause the organism to react in an expedient manner? To this there can be but one answer: because to react in this way is *the fundamental property of the living body*. But would such an answer satisfy the Darwinians? We think not. For if all living beings do possess the capacity of reacting to stimulation in a fit manner, what would be the use of natural selection? In that case, everything needful would be acquired at once.

Plate then proceeds to consider how great may be the probability of a coordinated occurrence of characters, if, as is done by Weismann, Wallace and de Vries, the theory of the inheritance of acquired characters be rejected. Plate himself maintains the theory of the hereditary transmission of acquired somatic variations, but as regards a certain group of characters he is compelled to admit that use or disuse has no effect on that transmission. To such characters are referred the so-called *passive* adaptations, which stand in no connection with use or disuse, such as coloration, mimicry, the spines of the hedgehog and the porcupine, the hinge of the shell of the bivalve molluscs, the various spines of fish, etc. Use and disuse, further, play no part in the production

of morphological and instinctive adaptations in sexless worker bees and ants, as such features appear simultaneously after the last moult (the instincts of young bees are in no way due to instruction).

If acquired characters are not transmitted through inheritance, the question of the coordination of characters becomes much more complex, for useful variations cannot fail to be reflected in germ cells, with the consequence that an accidental coincidence of useful variations will be very much less likely to happen. Nevertheless, says Plate, even if we admit this, the possibility of natural selection is not ruled out. Certain agencies facilitate the occurrence of needful combinations. To such may be referred the phenomenon of simultaneous correlative variation, when organs which function together very often vary in the same direction. Thus, if the bones of the limbs elongate, so do simultaneously the muscles, nerves and vessels (p. 212).

But this reasoning contains the same *petitio principii* as before. For Plate would hardly be ready to admit that with the increase in the length of the bones the nerves, vessels and muscles are simply stretched out, like worn-out clothes or old boots: in nerves, vessels and muscles occurs a purposive growth of their respective cellular tissue, in full coordination with the growth of the bones.[1] That is the very problem which requires solution, and must be accounted for. And yet the answer offered by Plate is substantially as follows:—the simultaneous occurrence of a series of useful characters is facilitated by correlative variability, *i.e.* by the capacity of the organism to react in a purposive manner. In other words, the organism acts purposively because it possesses, to use the language of Molière, the *virtus finalis*. Would it not be appropriate to recall here Pascal's ironical

[1] In chap. xxiv of his "Variation of Animals and Plants" (1868, p. 300) Darwin says, "It is well known that, when an artery is tied, the anastomosing branches, from being forced to transmit more blood, increase in diameter; and this increase cannot be accounted for by mere extension, as their coats gain in strength."

definition of light,—" la lumière est un mouvement luminaire des corps lumineux " ?

> Plate ("Selektionsprinzip," p. 134) gives another example of the effect of use. The flying membrane of the flying marsupials, flying squirrels (Pteromys), Galeopithecus and bats has arisen by the ancestors of these animals, while leaping from branch to branch, stretching out their fore-limbs and so subjecting to stimulation the skin of the sides of the body: in this way a fold of skin was formed. As a consequence of an adaptation to the *new conditions of life, the stimulation increased and the* fold grew bigger, until it was transformed into a parachute. Such is the opinion of Plate.
>
> But this fold is no simple mechanical resultant of the process of extension ; it is a complex organ with numerous nerves and vessels, an organ constructed so as to be fully suited to its functions. The formation of the flying membrane is not a mechanical, but a purposive reaction of the organism.

The following reflections of Plate serve still further to confirm our point of view. " Numerous observations of selectionists strengthen the opinion that every organism is to a certain point endowed with a capacity for self-adjustment (*Selbstregulierungsvermögen*), contributing towards the harmonious growth and variability of the parts of the same organ. If a plant is grown in heavily manured soil, it may attain a great size, while at the same time preserving inviolate the usual proportions of its parts, so that its general form remains unchanged " (pp. 212-213). But does it not seem to the reader that this capacity for self-adjustment is not widely separated from the *nisus formativus* of Blumenbach (1787), the *principle of " perfectionnement "* of Nägeli, the *vital force* of the vitalists and the *élan vital* of Bergson ? It is true that Plate endeavours to account for this property of the organism : if the capacity of coordination fails in an individual, the latter has to pay the price by being eliminated by natural selection. But this reasoning, when brought to its logical conclusion, renders natural selection itself quite

superfluous. And indeed, if Plate's point of view[1] be shared, it might then be assumed that the primary organisms which had accidentally possessed the capacity for reacting in a purposive manner and perfecting their organisation have survived and continue to exist, while the remainder have perished. Such an hypothesis, while denying the importance of natural selection in the recent historical and geological world, would set back its application to the time of genesis of life on earth.

Plate himself is obliged to confess that the nature of correlative variation is obscure (p. 223) and the physiological basis of adaptation is enigmatic (pp. 343, 596).

Without the principle that I uphold, Lamarckism has no importance in explaining evolution. This circumstance has apparently been lost sight of by many who have written in relation to Lamarckism, and it chiefly refers to those selectionists who, like Lamarck, attribute much importance to the use and disuse of organs.

Plate ("Selektionsprinzip," p. 592) thinks that the above-mentioned law of Lamarck, as it refers to both purposive and non-purposive characters, is a "causal and mechanical" law. But, it might be asked, where in the whole organic world are organs under normal (not pathological) conditions made use of otherwise than in a purposive manner? It is generally true that whenever organs are used, they are used in that manner.

If the principle of use and disuse be accepted, the hypothesis of selection, as we have seen, becomes entirely superfluous. For, if an organism is able to act in a purposive manner by the use or disuse of its organs, what is to prevent it from conducting itself in an absolutely identical manner, when, for instance, the need for the production of a *new* organ presents itself? The theory of selection, moreover, does not undertake to account for the *origin* of characters:

[1] In my opinion, a living organism that does not possess the capacity of responding to stimulus in a purposive manner, is a *contradictio in adjecto.*

it only attempts to explain why individuals endowed with useful characters survive and become more perfect. It would be possible to reason somewhat as follows. The contrivances of orchids for fertilisation by insects are exceedingly useful for the plant. How they originated is quite another question. But as soon as they have appeared the organism increases their efficiency through the same faculty that is manifested, let us say, in Proteus. This amphibian possesses both lungs and gills; if the animal is obliged to live in deep water, the gills grow to thrice their normal size, the lungs partially atrophying; conversely, in shallow water the lungs become larger, and the gills are reduced (this case is mentioned by Darwin, "Variation of Animals and Plants," ii, p. 297). The wonderful contrivances which are exhibited in the flower of orchids might likewise be produced by a similar capacity to react in a purposive manner.

Thus, to be consistent, anyone *should* reason who had once accepted the principle of Lamarck.

We mean, in short, that the admission of the principles of use and disuse, as also of adaptation to the environment, is a veiled acknowledgment that primordial fitness is inherent in every living body.[1] In such a case, the theory of selection becomes quite superfluous.

Meanwhile Darwin and his followers resorted to the principle of Lamarck in order to find an explanation for the most wonderful contrivances of the organism. Thus Darwin draws attention to the fact that if one kidney is destroyed, the other often replaces it by increasing in size and doing double work; if a portion of one bone of the leg or fore-arm of an animal (for example, the tibia of a dog) is removed and is not replaced by growth, the associated bone (in the above-

[1] It is remarkable that such an argument was perfectly clear to Kant. The celebrated philosopher maintained that the four human races had been derived from one common "genus" through the influence of climatic conditions. That hypothesis, he said, necessarily implies the capacity for development in man, *i.e.* an original predisposition to react in a different manner under varying climatic conditions. *The predisposition itself eludes a causal explanation.*

mentioned instance, the fibula) enlarges until it attains a bulk equal to that of the bones of which it has to perform the functions ("Variation of Animals and Plants," ii, 1868, pp. 300, 296).

It is remarkable how, as time went on, Darwin attached increasing importance to Lamarckism. The great naturalist was at first prone to overestimate the value of natural selection. Thus in 1861 (April 30th) he wrote to T. Davidson:

> "My greatest trouble is, not being able to weigh the direct effects of the long-continued action of changed conditions of life without any selection, with the action of selection on mere accidental (so to speak) variability. I oscillate much on this head, but generally return to my belief that the direct action of the conditions of life has not been great. At least this direct action can have played an extremely small part in producing all the numberless and beautiful adaptations in every living creature."[1]

In a letter to Hooker on November 24th, 1862, Darwin seems to be somewhat more disposed towards attributing greater importance to the effect of the environment:

> "I hardly know why I am a little sorry, but my present work is leading me to believe rather more in the direct action of physical conditions. I presume I regret it, because it lessens the glory of Natural Selection, and is so confoundedly doubtful. Perhaps I shall change again when I get all my facts under one point of view, and a pretty hard job this will be" ("Life and Letters," ii, p. 390).

Yet, in spite of the hope expressed in the concluding sentence, Darwin, as time went on, attributed increasing importance to the direct action of the environment. In the sixth edition (1872) of the "Origin of Species" (p. 421, chap. xv) Darwin made the following interpolation:

> "Species have been modified . . . chiefly through the natural selection of numerous, successive, slight, favourable variations, *aided in an important manner by the*

[1] "Life and Letters," ii, p. 369.

inherited effects of the use and disuse of parts;[1] and in an unimportant manner, that is in relation to adaptive structures, whether past or present, by the direct action of external conditions, and by variations which seem to us in our ignorance to arise spontaneously. It appears that I formerly underrated the frequency and value of these latter forms of variation, as leading to permanent modifications of structure independently of natural selection."

It would further be necessary to compare the above with the preface to the second edition (1874) of the "Descent of Man."

In a letter to Moritz Wagner Darwin writes (October 13, 1876):

> "In my opinion the greatest error which I have committed has been not allowing sufficient weight to the direct action of the environment, *i.e.* food, climate, etc. independently of natural selection. . . . When I wrote the 'Origin' and for some years afterwards I could find little good evidence of the direct action of the environment; now there is a large body of evidence, and your case of the Saturnia is one of the most remarkable of which I have heard."[2]

Finally, in a letter to Melchior Neumayer dated March 9, 1877,[3] on the occasion of receiving his essay "Die Congerien- und Paludinenschichten Slavoniens" (1875), Darwin wrote:

> "It . . . is *by far the best case which I have ever met* with, showing the direct influence of the conditions of life on the organization. Mr. Hyatt, who has been studying the Hilgendorf case, writes to me with respect to the conclusions at which he has arrived, and these are nearly the same as yours. He insists that closely similar forms

[1] The italics are mine.

[2] "Life and Letters," iii, p. 159. In the first edition of the "Origin of Species" (1859), at the conclusion of chap. vi (p. 256), Darwin wrote that "in some cases" natural selection is aided by the use and disuse of parts and is "slightly affected" by the direct influence of external causes. In the sixth edition of the same work (1872, p. 167) the words "in many cases" are substituted for "in some cases," and "affected" for "slightly affected."

[3] "Life and Letters," ii, p. 232.

may be derived from distinct lines of descent; and this is what I formerly called analogical variation. There can now be no doubt that species may become greatly modified through the direct action of the environment. I have some excuse for not having formerly insisted more strongly on this head in my 'Origin of Species,' as most of the best facts have been observed since its publication."

Thus, in course of time, Darwin increasingly inclined towards Lamarckism. But, apart from that, *a veiled acknowledgment of the principle of the inherent fitness of the living being lies at the basis of natural selection.* And indeed, that theory is based on the following principles, which cannot be further analysed: (1) heredity, (2) variation, (3) struggle for existence. These principles are accepted as given, as something obvious and self-evident. At the same time they are all purposive: if there were no variation, no organism could adapt itself to varying external conditions; if there were no heredity, it would be impossible to fix acquired characters; and, lastly, the struggle for existence postulates the faculty of self-preservation.

Selectionism must thus, from the outset, acknowledge the occurrence in the organism of purposive faculties in the shape of heredity, variation and self-preservation. But against this it might be urged that all these faculties have arisen in consequence of the struggle for existence; those organisms which were deprived of the faculties named, could not exist, and only those survived which had accidentally happened to possess them.

But such reasoning rests on a vicious circle: for the struggle for existence is accounted for as issuing from these very three principles, and they are deduced from the struggle for existence. At the same time, a being that is not endowed with the properties of variation, heredity and self-preservation, can in nowise be called an organism. To be called such, it must already be distinguished by possessing variation, heredity and self-preservation, *i.e.* the

capacity for reacting in a fit manner. It may even be said that the principle of self-preservation already contains the conceptions of variation and heredity, it being indeed nothing but a synonymous term for the principle of fit behaviour: organisms realise the minimum of variation and maximum of heredity (*i.e.* stability) necessary for self-preservation. The principle of the minimum expenditure of force (established by Maupertuis and Euler) is thus confirmed by the behaviour of the organism.

The postulate of the fundamental and inherent fitness of the living being, adopted by us, admits the exposition of the doctrine of evolution without recourse being had to any metaphysical premises, whether vitalistic or materialistic. Claude Bernard expressed a view closely approximating to this when he wrote in his famous "Leçons sur les Phénomènes de la Vie" (Paris, 1878, i. p. 46). "We disagree with the vitalists, for the vital force alone, by whatever name we call it, can perform nothing. It is capable of acting only when the general forces of nature are at its disposal, and without these it is unable to manifest itself. We differ likewise from the materialists. Although it is perfectly true that vital phenomena always arise under the direct influence of physico-chemical conditions, yet these latter alone would be unable to combine and bring into harmony phenomena in the order and sequence that they especially affect in living beings." [1]

[1] "Nous nous séparons des vitalistes, parce que la *force vitale*, quelque soit le nom qu'on lui donne, ne saurait rien faire par elle-même, qu'elle ne peut agir qu'en empruntant le ministère des forces générales de la nature et qu'elle est incapable de se manifester en dehors d'elles.

Nous nous séparons également des matérialistes; car, bien que les manifestations vitales restent placées directement sous l'influence de conditions physico-chimiques, ces conditions ne sauraient grouper, harmoniser les phénomènes dans l'ordre et la succession qu'ils affectent spécialement dans les étres vivants" (Cl. Bernard).

2. ON THE SIMPLICITY OF THEORIES

It was long an admitted axiom, and is not yet entirely discredited, that "nature always acts by the simplest means," *i.e.* by those which are most easily conceivable. A large proportion of all the errors ever committed in the investigation of the laws of nature have arisen from the assumption that the most familiar explanation or hypothesis must be the truest. One of the most instructive facts in scientific history is the pertinacity with which the human mind clung to the belief that the heavenly bodies must move in circles, or be carried round by the revolution of spheres, merely because those were in themselves the simplest suppositions.

J. S. Mill, "System of Logic," Book v, ch. iii, § 3.

Darwin's interpretation is seductive above all by reason of its simplicity, and *simplex sigillum veri*, as we are taught in the proverb. The great Newton also thought that *natura simplex est.*[1] Yet at present, even in reference to the inorganic world, we regard the matter in a different light. The assumption that nature is simple is, in Mill's words, a "natural prejudice" or "fallacy *à priori*."

Phenomena and laws appear to be simple only when they are artificially made so. Even the most elementary physical phenomena, in order to be exactly defined in mathematical language, require such complex differential equations as to defy being solved by means of contemporary mathematics. "If," says Jevons, in his attractive "Principles of Science" (1877, ch. xxxi), "we were to select at random any mathematical problem from the total number which can be offered, there would be a very small probability that it could be solved by a mathematician." According to Herschel, every particle of which atoms are composed has to solve differential equations, which, if fully transcribed, would encircle the Earth with ciphers. The laws of gravitation of Newton are very simple, yet they failed to account for the irregularities in the movements of Mercury. The laws of Einstein (1915), which attempt to grapple with this problem, are very much more complex.

[1] This view was borrowed by Newton from Galileo, who claimed that nature always and everywhere makes use of the simplest means (*principium simplicitatis*).

"That kind of simplicity is good," says Lotze (1857), "from which multiformity actually arises; but simplicity is vicious, when it is obtained at the cost of simplifying facts." We may also recall the ironical aphorism of Nietsche —"He is a philosopher; that means, he understands things to be simpler than they actually are."

The opinion that simplicity is the mark of truth is very widely prevalent. But such a view is erroneous. The simplicity of a hypothesis, says the distinguished Russian philosopher Vvedensky ("Logic" (Russ.), 3rd ed., 1917, p. 347), merely testifies to its worth as a convenient instrument for application to scientific investigation, but it in no wise demonstrates its intrinsic truth. Other things being equal, every instrument, every auxiliary means, is so much the more useful, the simpler it is. But, as soon as a simple hypothesis, when no longer *useful*, ceases to be such an instrument, it should be abandoned at once, and exchanged for another, without regard to whether that be as simple or actually more complex.

We may ask, does selectionism continue to be a useful hypothesis? Can a further advance in science still be expected of it? Does it answer to our present conception of the Universe? The following pages will serve as an answer to these questions.

3. ON CHANCE

What is chance? Is it a refutation of causality?

By the theory of probabilities chance is defined as an event, "the existence or occurrence of which cannot be deduced with certainty from conditions and premises of which we are cognisant." In making use of the conception of chance we do not thereby deny the presence of a causal connection: "we merely acknowledge that such a connection in a given case, either wholly defies comprehension, or is so complex as to preclude us from going beyond a

simple assertion as to its occurrence " (Czuber). From this definition it follows that, when the causal connection is obvious, there can be no room for chance. Departing from such a premise, the following definitions may be given.

Chance is a concurrence of facts, which are not related *to each other* by means of cause and effect and do not depend on one common cause, and, consequently, have no necessary connection between them (Windelband).

Chance is a concurrence of phenomena occurring independently of one another, or of a certain complex of individual causes with a certain combination of causes of a general character (Kaufmann, p. 21).

Contingencies, happening in relation to any given object, represent all such varying effects experienced by it as do not arise from the relatively causal connection of the object with the environment (J. Orlov, p. 160).

According to Bergson (1909) a contingency merely objectifies the state of mind of the individual, who expects to find one kind of order, but encounters another.[1]

It is clear from the following that chance in no way excludes causality, understood as conformity to law. And when we apply to our views the name of Nomogenesis, in distinction to the Darwinian theory of Chance, or Tychogenesis, we have no wish thereby to attribute to the great scientist the idea that those chance variations, with which he had to deal, are not subject to the law of causality.

Darwin himself, in the beginning of Chapter V (laws of variation) of his "Origin of Species," said, "I have hitherto

[1] Similarly Holbach in his " System of Nature " (1770) has already said that order and disorder are abstract terms, and can have no existence in a Nature where all is necessary and follows constant laws. Order is nothing more than necessity viewed relatively to the succession of actions. Disorder in the case of any being is nothing more than its passage to a new order, to a succession of movements and actions of a different sort from those of which the given being was previously susceptible. Hence there can be neither monsters nor prodigies, neither marvels nor miracles, in nature. By the same reasoning, we have no right to divide the workings of nature into those of intelligence and those of chance. Where all is necessary, chance can mean nothing save the limitation of man's knowledge (cf. J. Morley, " Diderot and the Encyclopedists," vol. ii, 1886, p. 173).

sometimes spoken as if the variations—so common and multiform with organic beings under domestication—and in a lesser degree with those under nature, were due to chance.[1] This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the cause of each particular variation" (p. 106).

In the concluding chapter of the "Variation of Animals and Plants" (ii, p. 420) he expresses himself thus, "Although each modification must have its proper exciting cause, and though each is subjected to law, yet we can so rarely trace the precise relation between cause and effect, that we are tempted to speak of variations as if they spontaneously arose. We may even call them accidental, but only in the sense in which we say that a fragment of rock dropped from a height owes its shape to accident."

The fundamental law to which contingencies are subject is as follows: *contingencies exhibit a tendency to compensate each other.* Such a tendency may be exhibited in two different ways: either contingencies annul each other, and in that case the general result approximates to zero, or their effect is summarised, so as to produce a certain mean, the deviations from which alone tend to cancel each other.

The molecules of the gases of which air is composed are in a state of continuous motion in the most diverse directions, and have the most diverse velocities, from several centimetres to several hundred metres a second. The movement and velocity of every molecule is governed by chance. It might be expected that, under such conditions, the temperature of the air would vary within very wide limits. As a matter of fact, in consequence of the innumerable collisions of thousands of millions of molecules, the air maintains a certain mean temperature. Let us take another case. In Russia in the year 1908 1,200 millions of ordinary letters were carried by post; of these 27 in every million

[1] Earlier, in chap. iv, p. 64, Darwin explains that in the term "variations" "mere individual differences are included."

were without any address. A letter without an address is a pure accident. And yet in the year 1910, when the number of ordinary letters conveyed by post reached 1,500 millions, there were the same 27 letters per million without address (Kaufmann, p. 40). Thus is exemplified the law of large numbers.

Thus, as a consequence of the play of chance, a certain mean quantity may be obtained by statistical methods.

Were the number of hereditary variations infinite, they would consist of purposeful and non-purposeful variations, and either would be approximately *equally* distributed (for if there were a preponderance in favour of the former, there would be no longer a question of chance, but a cause acting in a definite direction would thereby be manifested). It would seem, then, that the statistical mean should be equal to zero. But the endowment with purposeful variations confers on their possessor a preponderance, and submits it to the action of the dynamical element, namely, to that of natural selection, which on the one hand insures a positive advantage to the adapted organism, and on the other enables it to advance.[1]

Thus, in admitting selection, there need be no objection on principle to evolution being based on chance variations. Evolution may be *logically conceived* in the presence of natural selection.

But for this to happen, we must postulate one requisite condition, a *conditio sine qua non* : there must be *an infinite number of inherited variations*, just as there was in the two examples given above—in the one, an infinite number of

[1] We subjoin a statistical illustration of the effects of the dynamical factor :—

Mean mortality in Russia *per decades pro mille*—

1861-70	1871-80	1881-90	1891-1900	1901-1909
39·0	36·2	34·5	32·8	29·9

Mortality steadily falls. The dynamic factor is exhibited in the improvement in the welfare of the agricultural classes and in the amelioration of the sanitary conditions of towns. A similar dynamic factor in evolution might be found in natural selection.

molecules continuously changing the velocities and directions of their movements ; in the other, a vast number of letters. It is obvious that in a space containing a limited number of molecules the temperature could not remain uniform. Equally so, in a small inhabited spot the number of letters *without* address could *not* be subject *to any* law.

But it would be absurd to suppose an infinite number of *inherited* variations in organisms.

4. IS THE NUMBER OF VARIATIONS INFINITE ?

Whenever change occurs in nature, the amount of activity required to produce such change is as small as possible.

MAUPERTUIS, 1746.

In nature just that and so much happens, which may and can happen, and what happens occurs in one manner alone.

MACH, " Prinzipien der Wärmelehre," p. 392.

Darwin believed that the variability of organisms is infinite. In the " Origin of Species " (chap. iv, p. 66), he says, " The ordinary belief that the amount of possible variation is a strictly limited quantity, is a simple assumption."

Testimony of Palaeontology. If the foregoing statement were correct, we should find an infinite number of unsuccessful and intermediate fossil forms. But palaeontology shatters this expectation in the most decisive manner. If we direct our attention to groups that have been well studied palaeontologically, as, for instance, to ammonites and the Equidae, we shall be convinced of the fact that there can be no question of an infinite number of variations from which a selection could be made, for that number is limited and the variations themselves range in a definite line.

The difficulty thus presented as regards the theory of selection was very clearly perceived by Darwin. In the beginning of chap. x of the " Origin of Species " he says, " But just in proportion as this process of extermination has acted on an enormous scale, so must the number of

intermediate varieties, which have formerly existed, be truly enormous. Why, then, is not every geological formation and every stratum full of such intermediate links? Geology assuredly does not reveal any such finely graduated organic chain; and this, perhaps, is the most obvious and serious objection which can be urged against the theory (of selection). The explanation lies, as I believe, in the extreme imperfection of the geological record" (pp. 264-265).

The palaeontological record is, in general, undoubtedly incomplete, but it would be wrong to exaggerate that incompleteness. A group of fossil remains occurs, in which evolution may be at present traced with exhaustive completeness. We allude to the molar teeth of reptiles and mammals, which have been fully studied by Osborn (1907).

The fundamental, primitive type of the molar teeth of mammals was tritubercular, as it was termed by Cope in 1883. From it were derived the majority of, if not all, the types of teeth of the higher orders of this class; this circumstance has been incontestably established in the case of the Insectivora, the polyprotodont marsupials, edentate Taeniodonta, carnivorous Creodonta and Fissipedia, Primates, Ungulata, Condylarthra and others (Osborn, 1907, p. 3). In different orders the molars assume various forms, and in many become very complex. Yet complexity grows in strict accordance with a law; supplementary tubercles, for instance, and the variations of these, appear in a determined order and a definite position, and amongst fossils, forms are unknown in which the tubercles and their variations occupy a position undetermined by law, or are set anyhow and at random.

We may further refer to the authority of the great palaeontologist and thinker Melchior Neumayr, who, while being a convinced adherent of the theory of selection, yet says in his admirable book "Die Stämme des Thierreichs" (1889, p. 115), "Variations do not spread out in all directions in a disorderly manner, but are, as a rule, limited in number."

It would be more correct to say that, although numbers of individual variations and fluctuations do in effect occur, from such phenotypical material nature cannot build new forms, none of such variations being inherited. For the production of new forms genotypical material, in other words mutations, *i.e.* inherited variations, is required. And we affirm that the number of mutations is so limited that there is no scope for selection to operate in.

Had infinite variations prevailed in nature, and had every organ varied in all directions, deformed beings and monstrosities would have become the rule, while normal beings well adapted to their surroundings would form the exception. But both the recent and fossil organic worlds clearly demonstrate that an enormous mass of individuals are well adapted for existence.

An organism is a stable system, in which a tendency towards variation is confined within certain limits by inheritance. This truth is self-evident. It would be impossible to conceive how such complex organs as the eye, the ear or the pituitary body could properly exercise their functions, if they were the seat of an infinite number of variations, from which it would be left to chance to select the most efficient. Such an organ would be unable to answer its purpose for a moment. Variations in the pituitary body would cause the production of monstrous forms, similar to those which have been pictured by Lucretius in the classical words of his poem (v, 837 *seq.*). Such monsters would occur in vast numbers, both as fossils and in the recent fauna and flora. But nothing of the kind has happened. Throughout, the history of the earth presents to us beings as well adapted to the circumstances of their time, as recent ones are to theirs. However far back we may follow the fossil records, says the well-known palaeobotanist D. Scott (1911), we shall never meet with badly adapted plants, only with plants adapted to conditions different from those of the present. Whenever the environment is the same, we

meet with adaptations exactly similar to those which occur at present. The leaves of the palaeozoic club-mosses Sigillaria and Lepidodendron possessed on their lower surface two deep grooves protected by hairs; in these grooves stomata were hidden. Identical structures are found in recent plants subject to drought: it is an adaptation to protect the plant from excessive evaporation. The long and narrow leaves of the Cordaiteae were supplied with parallel ribs of strong fibrous tissue running through the leaf near the upper and lower surface, in the position where the most resistance to bending could be offered. In recent monocotyledons we find identical adaptations.

Infusoria manage to grapple with the problems of life quite as successfully as anthropoid apes. Bacteria are no worse adapted to their environment than any of the most highly developed Compositae. Can it be supposed that a shark is more ill-fitted for its watery element than an eagle for life in the air? As has been remarked by G. Wolff (1898), it follows from the very definition of an organism that every living being is able to respond in a purposive manner to stimulation, and is therefore adapted to its environment.

Even the most elementary forms of life are very complex, and are not behind more superior organisations in their capacity for purposive reactions. According to the researches of Jennings (1906), unicellular organisms respond to the same stimuli as do the higher animals. Protoplasm, devoid of a nervous system, responds to the same stimulations as do the sense organs of Metazoa. Even the naked protoplasm of the amoeba reacts to all classes of stimuli to which higher animals react. The nervous system and the sense-organs are thus not essential to the perception of any special kind of stimuli. Voluntary actions, *i.e.* modification of activity produced without the application of external stimuli, occur in Protozoa, just as in Metazoa. The idea that voluntary actions are confined to the higher

animals only is quite erroneous; activity in Protozoa is fully as voluntary as in man. There is nothing to prove that the behaviour of the Protozoa and of the lower Metazoa is essentially different. "The behaviour of the Protozoa is neither more, nor is it less, automatic than that of the Metazoa: both are governed by the same principles" (Jennings, chap. xiii).

In short, in the organic world, even on the lowest steps of *the phylogenetic ladder, beings adapted to their environment* and very perfectly constructed are found everywhere. Nowhere are to be encountered monstrous forms, which would certainly have been met with, had infinite variability prevailed.

From the above it does not, of course, follow that organisms have, as a rule, attained the highest conceivable degree of perfection, and that it would be impossible to imagine beings still better adapted to the environment. The history of the Earth exhibits many examples of a gradual improvement in organisation, *i.e.* of a more perfect capacity for responding in a fit manner to excitation. Such a series, for instance, is presented by the vertebrates. But this case merely goes to show that the world knows no miracles; Nature builds exclusively by the aid of the laws of physics and chemistry, and good results can only be achieved gradually.

In proof of the infinite variability of organisms, referenee might be made to the instructive observations of Vavilov (1922) on the various forms of wheat, rye, barley and lentil,[1] which exhibit an extraordinary variability. But although polymorphism in this case is very great, it is due to a redistribution of the same characters, whereas the boundary-lines separating the different species, as in the wheats (*Triticum vulgare, Tr. compactum, Tr. spelta, Tr. durum, Tr. polonicum, Tr. turgidum, Tr. monococcum* and *Tr. dicoccum*) remain inviolable. Variation is thus not

[1] On the lentil, see paper by E. I. Baroulina (Russ.), from the laboratory of Professor N. I. Vavilov.

infinite: its limits may be foretold. And, what is of the utmost importance, the example of the Gramineae convinces us that variation is not arbitrary or accidental, but is *determined by law*: it is not due to chance that the common wheat (*Triticum vulgare*) contains forms bearded and beardless, white-, red- and black-eared, hairy and smooth, winter and spring, etc.: for the same forms, according to Vavilov, occur in the dwarf wheat and the spelt, and he finds much the same thing in other wheats, as well as in barleys, in rye, etc.

It is thought by some that the number of combinations of genes during fertilisation is so great that among them progressive ones may accidentally occur. Thus Schimkewitsch (1922) says, "In man, with his 24 chromosomes in the sexual cells, the number of possible inherited combinations is about 300 billions, not counting those which may have been due to the intercrossing of chromosomes, and to the hitherto enigmatic process of the formation of new genes." On this hypothesis the problem of the formation of characters is transferred from the organs and adaptations to the genes, *i.e. merely shifted further back*. But whence do these genes proceed, each of which corresponds, as a rule, to some purposive character? I must adduce here the competent opinion of Jennings (1922, p. 6):

> "In reproduction from two parents familiar to us in higher animals and plants, there is a mixing of different stocks, a formation of great numbers of diverse groups of the hereditary materials, with consequent production of a great variety of diverse offspring from a given pair of parents. This is the chief cause of the differences everywhere observable among individuals; differences formerly classed as variations and considered the material of evolutionary change. But such kaleidoscopic re-grouping of materials, the units of which are not changing, has no obvious relation with evolutionary variation; in the next generation a new grouping of the same material occurs, and so on indefinitely."

On evolution by means of hybridisation. There is yet another conception of evolution, and it is that new forms are produced by means of crossing (Lotsy, 1914, 1916[b]; Regel, 1912, p. 493 *seq.*; 1917). When we cross sufficiently allied forms, distinguished by several hereditary genes, all possible combinations of factors may be produced; part of the forms thus constituted, when self-fertilised or inter-crossed with their like, become constant. "As a consequence, an innumerable multitude of billions of theoretically possible independent constant hereditary forms could be produced." Now is the time for natural selection to exert its sway, by which the forms best adapted for life are spared and the others doomed to perish!

Similar arguments have been advanced by Loeb (1912). Moenkhaus has demonstrated that it is possible to fertilise the egg of each marine bony fish with the sperm of any other marine teleostean. It is true that the embryos so obtained lived but a very short time, but Loeb subsequently succeeded in keeping such hybrids alive for over a month. As the number of species of existing teleostean fishes is about ten thousand, it would therefore be possible to produce about 100 millions of hybrids, of which, however, but an insignificant number, viz. $\frac{1}{100}$ per cent. can live. In the experiments of Loeb it sometimes occurred that in the hybrids eyes, brain, ears, pulsating heart, blood and vessels were formed, but the animals perished from the circulation either not setting in at all (although the heart would sometimes beat for weeks), or if started, stopping very soon. The ova of echinoderms may also be made to develop by fertilising them with the sperm of molluscs and worms, but the hybrids thus formed are short-lived.

"It is therefore no exaggeration to state that the *number of species existing to-day is only an infinitely small fraction of those which can and possibly occasionally do originate, but which escape our notice because they cannot live and reproduce.* Only that limited

fraction of species can exist which possesses no coarse disharmonies in its automatic mechanism of preservation and reproduction. Disharmonies and faulty attempts in nature are the rule, the harmonically developed systems the rare exception. But since we only perceive the latter we gain the erroneous impression that the 'adaptation of the parts to the plan of the whole' is a general and specific characteristic of animal nature, whereby the latter differs from inanimate nature."

"If the structure and the mechanism of the atoms were known to us we should probably also get an insight into a world of wonderful harmonies and apparent adaptations of the parts to the whole. But in this case we would quickly understand that the chemical elements are only the few durable systems among a large number of possible, but not durable combinations" (pp. 25-26).

Such a line of argument, following that of Lucretius and Diderot (and in saying this we do not wish to disparage Loeb), is founded on correct facts, but the author completely loses sight of the circumstance that all the hybrids of which he speaks are not of the least importance in the mechanism of the formation of species, for the probability of a hybrid being produced in nature from different species of marine fish is exceedingly slight. And if such a hybrid did appear, the probability of its surviving is still less, as, even in the artificial conditions of the laboratory, hybrids survive a month at the most, and then only in exceptional cases.

Furthermore, hybridisation, with the most insignificant exceptions, is successful only when crossings are confined within the limits of one species. Hybridisation thus leaves the boundaries of the Linnean species intact.

Lastly, in many animals hybridisation hardly ever occurs; it is rare in mammals, birds and reptiles.

The foregoing compels us to assume a negative attitude towards attempts to regard all the diversity of the organic world as the result of hybridisation, although we cannot deny that in certain cases hybrids may have constituted a basis for the production of new forms, as, for instance, in the

case of crosses between *Viola tricolor* L. and *V. arvensis* Murr., studied by Clausen (1922).

5. THE IMPROBABILITY OF "SELECTIONISM"

All modern natural science, says H. Poincaré, is nothing more than an unconscious application of the theory of probabilities. The naturalist is obliged to *weigh* probabilities. Laplace extends this principle to life, as a whole: "the greater part of the problems of life," in his opinion, "are problems of the theory of probabilities. Before solving them man has to sift a number of all possible cases, and, guided by common sense, he qualifies the various degrees of probability of each, and acts accordingly."

As a case in point, what is the probability of the test in the appendicularians (free-swimming tunicates) being accidentally formed? These animals inhabit a very complicated test, which is secreted by peculiar large epithelial cells, known as oikoplasts. In *Oikopleura albicans* the test is provided with a sieve for filtering minute organisms of the nannoplankton, an entrapping apparatus, a funnel, etc. Among the oikoplasts of this appendicularian there are two large groups—one for the secretion of the entrapping apparatus, another for the formation of the sieve (Lohmann, 1909). The test may be cast off and formed anew several times during one day, being secreted by the ectoderm. Can such a chance variation of two groups of cells be conceived, as should lead to the formation of a purposive apparatus harmonious in all its parts?

If we share this point of view on probability, we are bound to say that the probability of an accidental occurrence of even one useful character in such a complicated organ as the eye, the ear or the brain is insignificantly small. A new character, accidentally produced, is very likely to *injure* a complex mechanism; to expect that it will *improve* it would be in the highest degree injudicious. But probability

will very nearly approach zero, if we remember that an accidental variation of one character is insufficient for that purpose: a useful variation in the retina, for example, should be connected with variations in the whole apparatus simultaneously: not only a series of other parts of the eye, but likewise the corresponding centres in the brain should vary in the direction of usefulness. The probability that all useful variations will simultaneously occur in all the parts, is the probability of a miracle. Repeating Darwin's words, it might be said, "To admit all this is, as it seems to me, to enter into the realms of miracle, and to leave those of science."[1] We might just as well expect that if the wheels, screws and other component parts of the mechanism of a watch were to be put into a vessel, we could, by the simple process of shaking, get them to combine in such a manner as to become a watch that would function as such.

We may quote here the words of Whitman (1904, reprinted 1909, p. 12):

> "To assume that the eye began in some different variation that fluctuated or mutated, chance-wise, into a state of incipient utility, and was then developed in a direct line to its present stage of complex adaptations, either gradually or per saltum, would be hardly more satisfactory than appealing to a miraculous succession of miracles. It is impossible to believe that such a system of harmonious co-adaptations could ever arise by mutation."

Such is the matter from the theoretical standpoint. As to its practical side, palaeontology shows that new variations appear in a definite place and in a definite number (cf. Osborn *supra*). They may either be indifferent in relation to the organism, or they may be injurious (in which case the species eventually becomes extinct), or they may be useful. If they are useful, they are not so accidentally, but have occurred in a perfectly definite position, which was necessary for the organism.

[1] "Origin of Species," sixth edition, p. 204.

Selection has nothing to operate upon. This can best be seen in the examples of development in a definite direction, which we shall give later in the case of the Theromorpha, dinosaurs and pterosaurs.

In admitting the chance variations of Darwin, it is assumed that species possess the capacity for development in diverse directions.[1] We, on the other hand, drawing our inferences from the facts of palaeontology and comparative anatomy, assert that the course of development is predetermined by the chemical structure of the albumens of the given species (see chap. ii-iv).

Finally, Darwin took into account the variation of already existing characters. But very often we perceive the formation in organisms of *new* characters, occurring just in the position where they are needed. Let us give an example: in the pterodactyl the pneumatic foramen of the humerus lies in the same place and has the same size and shape as in birds. Can it be assumed that this foramen was formed at random anywhere on the humerus, and became fixed by selection just at the time when it accidentally blundered into the position it now holds, and where it can be of use to the organism? Such a supposition is really incredible. In the pterodactyl and in fossil, as well as in living birds, this orifice is always found in the same spot. True, it somewhat varies in shape, size and position, but within strictly defined limits. To anyone who has studied palaeontology, it is clear that from a number of variations an accidentally useful one could not have been selected by chance. In the case referred to, the new variation which proved to be useful occurred in the very position where it was needed by the organism. In the same way all characters are formed, *i.e.* in a definite position and in a definite shape.

This phenomenon may be accounted for in various ways, but no naturalist should close his eyes to facts.

Selection is, therefore, an improbable assumption, for it

[1] Cf. Plate, "Selektionsprinzip," p. 197.

attributes to chance a function which chance, according to the theory of probabilities, cannot possess.

Quite a number of authors, such as C. E. von Baer (1876), Strakhov (1887), Kölliker (1872), Nägeli (1884), Danilevsky (1885), Eimer (1888), Bekhterev (1916), O. Hertwig (1916) and many others, perceived the dominating rôle attributed to chance in the theory of selection, and consequently rejected selectionism.

But so long ago as 1746 Diderot objected to this in his "Pensées philosophiques" (§ xxi) by stating that a slight probability is compensated for by the number of combinations: matter exists and moves eternally, the world is infinite, atoms are numberless.

According to the computations of Laplace, the probability that the regularity of the planetary orbits is due to chance is approximately as 1 : 537,000,000. How many times less, asks Wundt (i, p. 319) is the probability of the accidental origin of living beings? It is believed, he says, that the probability of an accidental origin of purposive contrivances would be increased if the vast intervals of time were taken into account; but one forgets that time increases the number of unfavourable, as well as of favourable, variations.

The struggle for existence not only fails to produce useful characters, but in itself undermines the foundation upon which they are raised. For it destroys innumerable quantities of individuals: it is estimated that in a beech plantation the number of ten-year-old trees is 800,000-1,000,000 per hectare, and of trees 120 years old only 500-750 (Morozov, 1912, pp. 18-19). Had there been no struggle for existence, and had all trees produced seeds, the probability of the *accidental* occurrence of a new useful variation in the beech would be many times greater than under the operation of the struggle for existence: in the latter case, the useful variations might perhaps have appeared, but the individuals endowed with them would have perished.

It may happen that, if not an infinite, still a very large,

number of hereditary variations sometimes arise. This happens in the case of sub-species. When we pass from a region of the distribution of a typical species into a region where the latter is replaced by a sub-species, we may encounter a series of gradual transitions between the two. Thus an imperceptible series of transitions is observed to lead from the European chub (*Leuciscus cephalus*) to the Caucasian (*L. cephales orientalis*) and from the European fir (*Picea excelsa*) to the Siberian (*P. excelsa obovata*).

But such hereditary variations are not due to the action of natural selection ; they are due to the effects of the geographical environment (landscape) ; they are limited to a well-defined area, and are subject, as we shall see, to simultaneous variations in vast numbers of individuals.

6. DIRECT ADAPTABILITY

Let us suppose that we are obliged to select a key to fit a lock. We might take a bunch of keys we had accidentally found, and one of these keys might chance to fit the lock. But the lock might be opened by a key specially made for the purpose. In both cases, the opening of the lock would be due to the law of causality, all the laws of mechanics being duly observed, and this notwithstanding the fact that in the first case the key had fitted the lock by pure accident.

In like manner, Darwin assumes that the variability of organisms is so great that chance, in adapting characters (in a manner analogous to that in which the opener of the lock fitted his keys), will always select an accidental variation which may prove useful. Selection operates on accidentally useful variations. We, on the contrary, think that a useful variation arises just where it is needful, as a French lock is opened by its specially designed key.

According to Darwin's doctrine adaptation, cannot originally arise as the direct outcome of the vital activity of the organism : purposive adaptation develops as the consequence

of a multitude of variations of which one *accidentally* appears to be useful. According to this theory, every purposive manifestation of the activity of the organism should possess a very long history: those individuals which were not favourably endowed have perished, whereas their more lucky compeers, possessed of the needful qualities, have survived, leaving a well-equipped progeny.

Such, however, is not the case. We know at present of many instances, where adaptations are exhibited by the organism in conditions such as we know it was never subjected to in the whole former history of the species. These adaptations, to which we shall soon refer, are exhibited spontaneously and immediately, without any intervention on the part of natural selection.

One of the most remarkable illustrations of the foregoing are the graft "hybrids," or so-called *chimaeras,* which have been fully studied only in recent years. So long ago as 1825 the Paris plant-breeder Adam, in grafting a shield of the bark of *Cytisus purpureus* on to the stock of *Cytisus laburnum,* remarked that at the point of union in one case grew a branch with characters intermediate between *laburnum* and *purpureus.* This branch was vegetatively propagated; and now *Cytisus adami,* as this graft hybrid was called, is not infrequently met with in botanical gardens. Its flowers are of a yellow-red colour, intermediate between the stock and the scion. The seeds of *Cytisus adami,* however, produce the pure *Cytisus laburnum.* Quite lately, Winkler and others have succeeded in obtaining graft hybrids of the medlar (Mespilus) and the hawthorn (Crataegus), of various species of Solanum, of the orange and the lemon, etc. Investigations have shown that at the point of grafting no fusion of the cells of the scion and the stock takes place; groups of cells, belonging to both plants, grow concordantly and *produce stems, leaves and flowers consisting of tissues furnished by the different plants.* (Fig. 1.) Thus plants were obtained, in which the leaves on the same branch

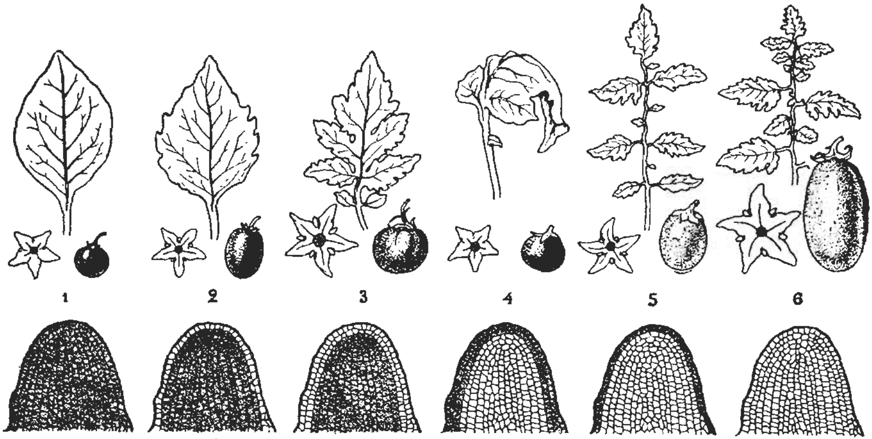

FIG. 1.—Chimeras, or graft hybrids, obtained by grafting *Solanum nigrum* on the common tomato, *Solanum lycopersicum*. For each plant are figured the leaf, flower, fruit, and a diagram of the longitudinal section of the point of growth. On sections the tissues belonging to *Solanum nigrum* are dark, those of the tomato are left white.

(From L. Jost, "Vorlesungen über Pflanzenphysiologie," 3 Aufl. Jena, 1913, G. Fischer.)

belong partly to the tomato (*Solanum lycopersicum*), partly to the nightshade (*Solanum nigrum*); and that was not all, for it sometimes happened that part of the same leaf belonged to the tomato and part to the nightshade. By the same process of grafting, it was possible to obtain fruits which were externally oranges, but were lemons inside, or were composed of alternating orange and lemon sections of the pulp. But what was even more wonderful, Winkler was so fortunate as to obtain a chimaera of this kind from a tomato and a nightshade, the leaves of which were intermediate in shape between those of the tomato and the nightshade, as if it constituted a veritable hybrid.[1] This seems as though some inner regulating principle had created forms out of parts of organs of two organisms.

Chimaeras have recently been recorded from the animal kingdom.

Spemann (1921) made the following experiment with two embryos of newts of two distinct species, *Molge vulgaris* (= *Triton taeniatus*, common newt) and *M. cristatus* (= *Triton cristatus*, crested newt). At the beginning of gastrulation he transplanted the ectoderm of the anterior extremity of that portion of the embryo of the common newt which gives rise to the central nervous system to that part of the embryo of the crested newt which will give rise to the epidermis. And, conversely, a section of the future epidermis of the embryo of the crested newt was transplanted to that part of the embryo of the common newt which corresponds with the future medullary plate. As the ectodermal cells of the embryos of both species are easily distinguishable by their different colours, there is no difficulty in following up the subsequent development of the transplanted parts. It appears that the transplanted tissues continue to develop although fully adapting themselves to the new position in which they were placed: the rudiment of the nervous

[1] On "chimaeras" see, for instance, Babcock and Clausen, 1918, pp. 374-384.

system surrounded by that of the epidermis in the crested newt develops into the epidermis, while the rudiment of the epidermis in the midst of that of the nervous system in the common newt ultimately forms part of the brain and eyes. Nevertheless, *the transplanted parts retain their specific characters in their new position, i.e.* although the tissue of *Molge cristatus* develops in *M. vulgaris* conformably to the requirements of the latter, it still retains the peculiarities of the tissue of the crested newt. Spemann compares the composite individuals thus obtained by him with plant chimaeras.

Issajew (1923) grafted together two hydras belonging to distinct genera: the local red *Hydra vulgaris* and the brown (or grey) *Pelmatohydra oligactis*. On the complantate could be seen the five to six long tentacles of *oligactis* and the six short ones of *vulgaris*. At first each group of tentacles contracted independently, but after an interval of a couple of days, a complete physiological union was established and all the tentacles contracted simultaneously. Prey was captured and assimilated as in the case of any normal hydra. Soon afterwards, however, the red substance disappeared and the complantate became grey, exactly like a typical *oligactis*. It might have been supposed that the *oligactis* had completely absorbed the *vulgaris*. But it was not so. In the budding of the complantate a remarkable phenomenon could be observed: as in the *vulgaris*, two, and not one (as in *oligactis*), buds simultaneously appear, being as in *vulgaris* opposite to one another. The third bud appeared singly, but with eight tentacles, which number never occurs in the buds of *oligactis*. In all the cases, the tentacles appeared simultaneously, as in *vulgaris;* never in pairs, one after another, as is the case with *oligactis*. The buds of the chimaera, in general, gave rise to two kinds of hydras: (1) differing in nothing from the *oligactis* and producing a progeny of pure *oligactis*, and (2) intermediate between *oligactis* and *vulgaris* (called by the writer "oligactoid"), which gave rise to pure *oligactis* and oligactoid, the latter perceptibly predominating. We thus encounter, as it were, a case of a true graft hybrid.

Goetsch (1923), having united two hydras belonging to different genera (*Hydra attenuata* var. *viridescens* with *Pelmatohydra oligactis*). obtained a mosaic chimaera, which transmits its peculiarities to its buds (*i.e.* asexual reproductive organs).

It has been found possible to grow the anterior part of the earth-worm *Allolobophora terrestris* on to the posterior part of another species, *Allolobophora foetida*. The anterior part of the pupa of the moth *Saturnia cynthia* has been united with the posterior part of that of *Saturnia promethea*; from the creature made up in this manner, a moth was hatched. The union of the anterior part of the frog, *Rana virescens*, with the posterior part of that of *R. palustris* was also successful: from such twin embryos tadpoles were hatched, which eventually grew up to be young frogs, half *virescens* and half *palustris* (Harrison, 1898).

Both in the case of vegetable "chimaeras" and in that of animal transplantation just described, a single organism was obtained, responding in a purposive manner to stimuli. As in their former (phylogenetic) experience the individuals selected for grafting or transplantation had never encountered anything of the kind, it obviously follows that the capacity for reacting in a purposive manner is commonly developed, not as a result of natural selection, but owing to that capacity being originally inherent in the organism.

The retina of the eye, as is well known, is formed as the product of the differentiation of the optic vesicle, which is a hollow outgrowth of the fore-brain. The lens, on the other hand, is derived from the skin situated over the optic cup. Spemann (1912) transplanted the optic cup of the embryo of Salamandra by inserting it under the skin in another part of the body, and it continued to develop; but what is especially deserving of note is the fact that in the skin above the transplanted vesicle a lens was formed, as if the eye had developed in its normal position.

Filatoff (1916, p. 51) transplanted the auditory vesicle from one embryo of Bufo to another at the same stage. The vesicle was transferred into the mesenchyme between the auditory vesicle and the eye. Nearly always a carti-

laginous auditory capsule developed from the cells of the *mesenchyme*. The material for the capsule is not predetermined: it develops from any mesenchyme cells which happen to be in the neighbourhood of the auditory vesicle.

As regards these last examples, the question might be raised, whether the behaviour of the transplanted optic cup or auditory vesicle was purposive; but one thing, in any case, is clear—the organ develops in a position and under circumstances such as it had never encountered in the whole history of the species. And yet it at once assumes the form natural to it.

Lastly, we may refer to the phenomenon of artificial immunity, when the organism acquires the capacity to react in an efficient manner under the influence of substances with which it had never before come into contact.

All the foregoing examples, and the number might easily be increased, do not seem to leave any doubt that the organism is capable of acting efficiently, without having been trained thereto by previous individnal or inherited experience.

If such be the case, many other contrivances, which are known to have recurred in series of generations, very possibly do not require to be accounted for by the hypothesis of the selection of accidentally useful characters.

Thus it has been demonstrated in the laboratory of Professor I. P. Pavlov that each kind of food causes in the mouth the secretion of saliva of a perfectly definite chemical composition, suitable for the proper transformation of the former. The same is true of the functions of the digestive glands: when bread is being consumed, the secreted gastric juice is richest in pepsine; it becomes poorer in that enzyme when meat is introduced, and still poorer in the case of milk. In childhood the intestine secretes lactase, a ferment which decomposes lactose: in the adult, lactase is generally absent. Chymosine, a ferment that coagulates milk, is exclusively produced in the gastric glands of the calf, the foal and the

sucking pig, during the period of suckling, disappearing when the animal becomes self-supporting. According to the observations of Koldaev (1916, p. 1032), the amylolytic, or starch-digesting ferment of the calf is several times weaker than that of the adult animal; this may be explained by the fact that the calf, while feeding on milk, of all the carbohydrates receives only lactose, and does not require amylase, a ferment that digests starch. Moreover, in the dog, a carnivorous animal, amylase is characterised by its very feeble action; in the omnivorous pig it is stronger; in the herbivorous animals it is stronger still.

Plate, in his "Selektionsprinzip" (1913, p. 561), very graphically illustrates the difference between Lamarckism and Darwinism. It is obvious, he says, that in normal conditions every organism should react in a purposive manner, for its entire organisation is adapted to these normal conditions. But how will the organism behave when it is transported into a perfectly new environment, in which neither it nor its ancestors had ever been placed? In that case a new purposive reaction or adaptation has to be evolved, or else the organism will perish. Now, the Lamarckians assert that in such a situation the new adaptation appears *spontaneously without the aid of selection*: all or nearly all the individuals vary at once in the required direction. In the opinion of Darwinians, on the other hand, individuals behave in various ways: only a small number of them react in a purposive manner and survive in the new environment, the majority perishing; in this case adaptation has been evolved in an indirect manner, by the aid of selection. The discrepancy between these views, says Plate, is not absolute and fundamental, but is superficial, being based *on quantity*.

But, as a matter of fact, the discrepancy, we say, is immense. And any unbiased consideration of the facts leads to the conviction that new adaptations are not produced in the way which was conceived of by Darwin.

7. VARIOUS TYPES OF THE STRUGGLE FOR EXISTENCE

Together with Plate (*Op. cit.* 1913, p. 223) we may distinguish the following types of the struggle for existence, or, in his words, of "natural elimination."

1. *Catastrophic extermination in the mass.* In this case no account is taken of superiority of organisation; both the bad and the good are equally destroyed: this type has, therefore, no importance in the process of evolution. To this type may be referred the extermination of individuals, eggs or seeds by floods, volcanic eruptions and tempests, and wholesale consumption by the whale of millions of copepods at one gulp, etc.

2. *Individual selective extermination* due to an imperfect adaptiveness on the part of individuals. It is alleged that this type leads to natural selection and the survival of the fittest. The destructive agencies in this type are:

(*a*) Inanimate nature, *i.e.* climate, soil, etc. To this type of destruction alone Beketov (1896, p. 14) would like to apply the term of struggle for existence. Wundt (i, p. 317) truly remarks that, in the view of Darwinians, the struggle for existence in this sense is but the continuation of the play of chance effects, which is at the root of Darwin's conception of infinite variability.

(*b*) Plants and animals of other species; this involves the struggle between species.

(*c*) Individuals of the same species (or sub-species, "natio," etc.), or struggle within the species, or, as Beketov calls it, vital competition. This struggle, according to Darwin, is the severest, as occurring between individuals having, as a rule, the same needs ("Origin of Species," chap. iii, p. 59).

In distinction from the struggle with the inorganic world (*a*), the struggle with organisms for food and reproduction (*b* and *c*) is based, in animals at least, on an active principle, the will. The element of chance must, therefore, be

relegated to a secondary position. Darwinism, to a certain extent, here adopts the ideas of Lamarck: the organ is perfected by the exercise of its functions (Wundt, *l.c.*).

Of course, the struggle for existence, as a fact, cannot be denied. It must not, however, be forgotten, that in the organic world, besides the struggle for life, an important place should be reserved for a principle of opposite tendencies, that of *mutual aid and love*, to which attention has been drawn by the Russian naturalists Kessler (1880) and Kropotkin (1890).[1]

But neither the struggle for existence, nor mutual aid, can be regarded as factors of somatic evolution in the organic world. Evolution follows strictly determined laws, without being affected by the struggle for existence or by mutual aid.

8. PART PLAYED BY SELECTION

1. In chap. iv of the "Origin of Species" (pp. 70-71) Darwin gives the following illustration of the action of natural selection. The wolf feeds on deer. Suppose that the fleetest deer were those which had mainly increased in numbers, or that other prey of the wolves had decreased in numbers during that season of the year when the wolf was hardest pressed for food. "Under such circumstances, the swiftest and slimmest wolves have the best chances of surviving, and so be preserved, or selected."[2]

This reasoning is perfectly correct. But, and in this lies one of the most essential objections to the hypothesis of

[1] Mutual aid, even if only in a slight form, is to be met with among plants. Thus, trees growing in forest associations are successful in resisting unfavourable climatic conditions, such as winds. (Cf. Beketov, 1896, p. 19.)

[2] Compare also "Variation of Animals and Plants," ch. xx, p. 221. The giraffe "might have its neck, or head, or tongue, or fore-limbs elongated a very little . . . and animals thus slightly modified would, during a dearth, have a slight advantage, and be enabled to browse on higher twigs, and thus survive. By the repetition of the same process, and by the occasional inter-crossing of the survivors, there would be some progress, slow and fluctuating though it would be, towards the admirably coordinated structure of the giraffe."

natural selection, these swift-footed wolves will produce a progeny consisting not only of the swift-footed kind, but of *the slow-footed also*, and the proportion between both, or their average speed, will be the same in the progeny of the swift-footed individuals as it was before the experiment performed by natural selection.

And yet there is one case in which selection might be effective, *i.e.* when among the wolves there were already two forms, swift-footed and slow-footed. In such a case, races which had existed previously might be segregated or isolated. But then the questions as to how these races were produced, and what was their former evolution, rise again before us. And it becomes clear that here selection had possessed no creative power. As was shown by Johannsen in his experiments with beans, and by Jennings with Paramecium, selection within the limits of a pure line is powerless. And whenever selection produces any results, it means that the organisms experimented upon were composed of several pure lines, every one of which possessed its particular inherited characters. But such a mixed population cannot produce anything *new*, anything that had not been previously inherent in it, however long we may continue to resort to selection for this purpose. And that is not all. By means of selection it is never possible to overstep the limits of variations that are peculiar to a pure line.

Plate (1913) agrees with these inferences, but holds that selection begins to assume its sway, whenever the organism, no matter how, has acquired a new character. But we may even grant the admission that in the process of time convincing cases of the effectiveness of selection within the limits of a pure line will be exhibited.

However that may be, all that we hitherto know with regard to pure lines shows, according to a true observation of Jennings (1910, p. 144), that the cases with which selection has to deal are very rare events indeed. Such a lucky "case" *is a newly inherited and useful character.* To seize

on this new character, such is the all but insoluble problem which selection has to attack.

Besides the experiments of Johannsen (1903) with beans (*Phaseolus vulgaris*), which constitute the beginning of a new era, quite a number of more recent investigations have shown that selection within the limits of a pure line is powerless to produce anything new. In this connection we may mention the researches of Jennings (1908, 1912) on Paramecium, Hanel (1908) and Lashley (1915, 1916) on Hydra, Winslow and Walker (1909) on bacteria, Woltereck (1909) on Daphnia, Agar (1913, 1914) on Simocephalus and on Aphides, Ewing (1914, 1916) on Aphis, Sturtevant (1918) on Drosophila, Surface and Pearl (1915) on oats, Fruwirth (1915) on lentil, pea, soy bean and lupin. We may also add the work of Vilmorin on wheat and of the Svalöf (Sweden) station on various Gramineae.

It would be only just to mention that quite lately the effects of selection have been recorded in the case of certain Protozoa. We refer to the researches of Jennings on Difflugia,[1] and of his pupils, Middleton (1915) on Stylonychia, and Miss Stocking (1915) on the inheritance of monstrosities in Paramecium. But it has yet to be ascertained whether the importance of these experiments in the question we are engaged in is as great as the adherents of the theory of natural selection would apparently wish it to be. Thus, in regard to Difflugia, it is probable that Jennings worked with material that was not genotypically pure. Pearl (1917, p. 86) offered the following very plausible suggestion: ordinary selection acts on somatic characters, and is therefore evolutionally powerless; but were it possible by means of selection to affect the germ plasm in a direct way, there would then be no ground for doubting the efficacy of such selection. In certain experiments with Difflugia, Jennings selected not merely individuals possessing a small number of spines, but notably such as *displayed a tendency towards producing offspring with a restricted number of spines.* In such a case, the successful application of selection was, of course, assured, because the very gametes which were required

[1] Jennings, "Genetics," i, 1916, pp. 407-534 (has not been seen by the author).

had been selected. Yet, says Pearl (p. 87) "in ordinary Darwinian selection we select that *kind of somata* we want, and trust blindly that a wise providence has implanted in them the sort of gametes we *need* in order to get further somata like those we selected." Thus, continues the same author, in the given instance we have a case which is completely parallel to the isolation of pure lines from a mixed "population": several individuals endowed externally (somatically) with the requisite characters are found; but experiment proves that these individuals fail to produce the sort of progeny we need; they are then cast aside and in their place others are selected, which reproduce their own peculiar characters; these individuals are retained.

Johannsen (1922, p. 100) likewise considers that in the observations of Jennings a segregation of *mutations* had taken place, the latter process producing an impression as if modification of the genotype had occurred by means of selection.

In the case of multicellular organisms with sexual reproduction we know many instances of the efficacy of selection. Positive results have been obtained by Pearl (1915) in his experiments on the increased reproductive power of hens, Smith (1908) and other workers on maize, MacDowell (1915) on the number of bristles in the fly Drosophila, Zeleny and Mattoon (1915) on the eyes of the same fly, Castle and Phillips (1914, 1916) on hooded rats.

Castle made experiments on the crossing and selection of hooded rats. They were black and white, or grey and white. In 1907 he started his experiments with a colony of twelve rats, crossing the blackest with the blackest and the whitest with the whitest. The blackest gave origin to the series +, the whitest to −. The blackest of the generation + were selected and crossed; so were the whitest of the generation −. In this manner sixteen generations + and seventeen generations − had been examined. It then appeared that the series + became increasingly blacker, and the series − whiter. By distributing the coloration according to artificial "grades," it became possible to compile the following table,

which is the result of experiments with 16,107 individuals :

No. of generation.	Mean "grade" of blackness in parents.	Mean degree of blackness in progeny.
1	2·51	2·05
3	2·73	2·51
5	3·33	2·90
7	3·56	3·20
9	3·78	3·54
11	3·98	3·78
13	4·13	3·94
16	4·45	4·13

It appears that the offspring are less black than their immediate parents ; still, owing to selection, the general degree of blackness steadily increases.

The experiments with the series – produced a progeny of 17,142. Of this number the white colour in the blackest lingered on only on the breast between the fore-legs, and the black colour in the whitest remained in the shape of a few spots near the eyes, ears and snout (Castle and Phillips, 1914).

However, subsequent experiments with selected hooded rats showed the inefficacy of all the previous selection work. Castle (1919) crossed the minus selected race (mean grade – 2·6) with a wild race. A third cross produced F_2 hooded young exclusively *plus* in character, mean + 2·5. Generally speaking, three crosses with a wild race "had sufficed practically to eliminate whatever differences had been produced in the minus and plus races respectively by long-continued selection in opposite directions" (Castle, 1919, pp. 129-130).

In all the above-mentioned cases, we do not know in how far the original material was homozygous. At any rate, Baur (1919) stated that hooded rats consist of a mixed population.

In the opinion of MacDowell (1915, pp. 94-95) the selection of the number of bristles on the thorax of Drosophila is effective so long as homozygotes in respect of "supplemental

factors" are not obtained. In general, this writer declares himself against the efficacy of selection. To this opinion incline both Zeleny and Mattoon (1915, p. 528), who have conducted selection experiments on the same fly as regards the number of facets in the eye.

Moreover, as has been pointed out by Pearl (1917, p. 88), there are grounds for assuming that only such individuals had been selected for experiment as exhibited a *tendency* towards the reproduction of a progeny bearing the desired characters.

But what, we may ask, induces individuals with desirable characters to inter-cross in a state of nature? No such agency exists. And even if the requisite progenitors were to interbreed by mere accident, what would be the chances for the retention by the progeny of the favourable characters and tendencies in all their purity?

Natural and artificial selection are two very different things. They agree in that they both *destroy* useless and needless forms. But this is not enough to account for evolution. To destroy what is unfit does not suffice; it still remains to select what is fit, and to combine the result, to compel the useful and the fit to multiply. But the latter can be accomplished only by artificial selection, in which acts the intelligent will of man. The creative side of selection is found in artificial, not in natural selection.

The recent researches of MacDowell (1917) on the selection of 49 generations of the fly Drosophila with a view to increase the number of its bristles, showed that selection was effective as far as the eighth generation, beyond which it was powerless to increase the number of bristles.

Finally, we may quote the opinion of such an authority as Castle (1921):—"The substance of our present knowledge as to changes in genes may be summed up in the statement that such changes come or go suddenly and in their entirety, and *cannot, as far as we know, be influenced by selection or any other controllable process*. Hence we may well call change in genes mutations" (p. 189).

Referring to his experiments with hooded rats, Castle says: "Repeated crossings with the non-hooded (wild) race had caused the changes in the hooded character, which had been secured by selection, altogether to disappear. This result showed conclusively that the changes in question had not occurred in the gene for the hooded pattern, but in the residual heredity. Other cases of apparent gradual change in unit-characters under the action of selection may be explained in a similar way. Accordingly we are led to conclude that unit-characters or genes are remarkably constant, and that when they seem to change as a result of hybridization or of selection unattended by hybridization, the changes are rather in the total complex of factors concerned in heredity than in single genes" (p. 185).

2. The most recent investigations of Vavilov concerning the winter and spring varieties of plants are remarkable.

The difference between these forms consists in that the spring varieties of cereals, on being sown in spring, flower and fructify in the same year: the winter varieties, even in southern climates, on being sown in spring, tiller vigorously, but produce no stems, do not flower or yield fruit; all this occurs in the following year, after a winter's rest. Heretofore, the view has prevailed that the winter races are the ancestors of the spring races; according to this view, the transformation of the winter plants into the spring races was due to selection, accomplished by man. Such is the opinion of Hildebrand (1882), Körnicke (1885), Wettstein (1897), de Vries (1901), N. W. Zinger (1909, p. 170), R. E. Regel (1910, p. 237; 1917, p. 180). The last-named points out that the wild ancestor of the cultivated two-rowed barleys, namely, *Hordeum distichum* var. *spontaneum*, is represented by winter varieties: all the spring barleys have originated since the historical period. While cultivated oats (*Avena sativa*) are represented by spring forms, wild oats (*Avena fatua* and *A. ludoviciana*), closely allied to the cultivated, are winter forms. The spring scarlet bean (*Phaseolus*

coccineus), according to Wettstein, owes its origin to the perennial wild bean.

Yet the most recent researches of Vavilov (1921) on the cross-fertilisation of the winter wheat *Triticum compactum* var. *wernerianum* with the spring *Tr. vulgare* var. *lutescens*, show that the above view is incorrect. The first generation represents the typical spring form ; the second already segregates, the greater part being spring forms, a part intermediate, and 10 per cent. winter. The progeny of some of the spring forms of the second generation continued to segregate into spring and winter forms. The type of segregation mostly recalls the dihybrid, *i.e.* crossings in which the inherited character is determined by two genes. However that may be, the character of the "spring form" behaviour manifestly dominates over that of the "winter form," the character of the winter form being recessive. Therefore, in spite of the widely-accepted view, the progenitors of the winter races may be spring forms (Vavilov, p. 20). Nor is this all, for the opinion that wild forms are exclusively winter forms has proved to be incorrect. In 1916 Vavilov collected in northern Persia and in the Transcaspian region specimens of the wild barley *Hordeum distichum* var. *spontaneum* ; when the plant was sown in spring in Moscow and Saratov, it appeared that spring varieties were present among the separate samples. The same appears to be true for the wild emmers (*Triticum dicoccum* var. *dicoccoides*), which are held to be the progenitors of cultivated wheats : amongst samples from Syria, in addition to winter forms, spring forms were found. The wild forms of the gramineous Aegilops, closely allied to wheat and unknown in the cultivated state, are represented in Persia, Bokhara and Turkestan both by winter and spring forms. The same applies to the wild oats *Avena fatua* and *A. ludoviciana*.

There can, therefore, be no doubt that winter forms did arise from spring forms. But, of course, the reverse may

also happen, *i.e.* the derivation of spring forms from winter forms. Spring forms may thus be both recessive and dominant.

Therefore, it was not the artificial selection of *accidental* variations that caused the transformation of winter into spring forms. Both the spring and the winter forms *have existed in Nature from the very beginning.* The rôle of selection is limited to the segregation of pure lines of spring races from mixtures of winter and spring forms, which are observed to occur among wild plants.

In the light of these investigations, the valuable researches of Zinger (1909) on the species of spurry, Spergula (of the Caryophyllaceae), which obstruct the growth of flax crops, acquire quite a new significance. These researches have brought out points that seem to prove the importance of selection. In the wild *Spergula vulgaris* and *Sp. sativa* the ripe capsules open widely, and thus readily shed the seeds, as so often happens in other plants. But in *Sp. maxima* and *Sp. linicola*, which grow among flax and are derived from the preceding species, the ripe capsules scarcely open, and the seeds are therefore retained. Such a structure would have been injurious to the wild species, as it would prevent the dispersal of the plant, but to a weed it is eminently beneficial, the capsules being threshed with the flax; and the seeds of the spurry are accordingly so mingled with the mass of the seeds of flax, that subsequently they get sown with these. *Spergula maxima* and *Sp. linicola* thus insure to their progeny a continued cohabitation with flax. Such a contrivance would seem to us simply miraculous, did we not acknowledge the unlimited capacity for variation exhibited by the parental species, *Sp. vulgaris* and *Sp. sativa.* And the following explanation might be put forward. Of the number of individuals of the spurry that happen to intrude into the flax crops, the progeny of those specimens would have the best chances of multiplying in which the seeds were not shed in the field.

Such specimens with almost closed capsules may have produced offspring, which would easily have re-invaded the flax fields. Those individuals, on the contrary, which were deprived of the faculty referred to, produced a progeny which for the most part perished. By this means were selected the spurries that do not shed their seeds. Yet the likelihood of the occurrence of such a favourable chance is exceedingly slight. An extremely wide range of variability has to be admitted for that purpose.

But, as a matter of fact, no such assumption is even necessary. The study of cultivated plants and injurious weeds shows that the capacity for producing fruit with capsules which do not shed their seeds, is exhibited by numerous plants. To be more explicit, a given species disintegrates into a series of forms, of which one (or several) is endowed with a capacity for not shedding its seeds. Such forms are not only most suitable for cultivation, but they also have the best chance of becoming weeds, injurious to cultivated plants.

Flax (*Linum usitatissimum*) is represented by several forms: in one (*L. crepitans*) the capsule opens automatically and the confined seeds are thus liberated; in another, which is the one most generally cultivated (*L. usit. vulgare*), the capsules do not open, and the seeds are set free only through the process of threshing.[1] The same feature, useful to a cultivated plant, occurs in one of the kinds of poppy (*Papaver somniferum β album* DC.).[2] Of the noxious weed shepherd's purse (*Capsella bursa-pastoris*), a mutation (sport) from Pfalz, Germany, with non-opening pods has been described.[3] *Alectorolophus major* sheds its seeds, whereas the weed infesting rye fields, *Alectorolophus apterus*, has closed capsules and the seeds are liberated only when threshed (Zinger, 1913). *Lithospermum arvense*, a weed injurious to both winter and spring crops, possesses a remarkable property: its fruit, on ripening, separates into four nutlets, of which

[1] De Vries, 1906, *pp.* 49-50; Zinger, 1909, *p.* 278.

[2] De Vries, 1906, p. 55; Zinger, *l.c.*

[3] De Vries, 1906, p. 356.

> three drop to the ground, while the fourth remains on the torus, from which it is detached while being threshed with the cultivated plant (Betner, 1917, p. 206).

It is obvious that plants already possessing the faculty of not opening their capsules find an advantage in becoming injurious weeds. There can, therefore, be no question of such a character having arisen by chance and subsequently becoming fixed through selection.

We may further observe that the cultivated, in distinction from the wild, forms of wheat, rye and barley possess strong rachides, which circumstance is of the greatest convenience in the process of threshing. Körner, in his " Life of Plants," asks why forms with strong rachides should not have been preserved in the wild state? To this Zinger (1907, p. 278) replies that wild forms possessing such a feature have probably never existed, but single specimens (mutations) with a tough rachis may have arisen from time to time; the character is injurious to the wild plant, as it impedes reproduction; but when cultivated, such specimens were intentionally selected, and gave birth to a stable race. And yet it is more likely that wheats, ryes and barleys, both with brittle and with strong rachides, should be found in the wild state, and that in this case, as in many others, we have to deal with a mixture of elementary species.

Here also there is no question of infinite variation. The character sought for had existed from the beginning. And a given form is fixed by artificial selection, simply because its peculiar character was useful to man.

> Another case is that of the cultivated hemp (*Cannabis sativa*), the seeds of which, as is well known, are not shed when ripe. The wild hemp (*C. sativa* var. *spontanea*), wrongly regarded as a quasi-spontaneous form of the cultivated plant, has been shown by Vavilov (1922, pp. 147-8) in south-eastern Russia to possess seeds provided at their base with a structure resembling a horse-shoe, at which point the seed, when ripe, or even slightly before, easily breaks off and is shed. A careful examination

of the wild hemp has revealed a number of forms, differing from each other in the colour, shape and size of the seeds and in the development of the "horse-shoe." Forms in which that structure is wanting are not infrequent. Between the true wild hemp and the typical cultivated plants occurs a series of transitional forms.

3. *Selection of Domestic Animals.* In England breeders habitually speak of an animal's organisation as something plastic, which they can model almost as they please. One of them, referring to what has been done in this matter in England with respect to the sheep, remarks, "as if they had chalked out upon a wall a form perfect in itself, and then had given it existence" (Darwin, "Origin of Species," chap. i, pp. 22-23; "Variation of Animals and Plants," chap. xv, p. 195).

But it is a great error to suppose that new races of domestic animals and cultivated plants may be moulded by means of selection, as if they were clay. "New" forms may be produced only when a given species possesses the requisite tendencies. But this has only become feasible because domestic animals and cultivated plants are derived from various wild forms and even species (the dog and wheat may serve as good examples),[1] and had consequently possessed highly diversified characters in their wild state. So that in this case the "new" is but a revelation of the old. This is perfectly clear when one considers, for instance, that it is not every breed of cattle which, by mere selection, can be transformed into a short-horn, nor every horse into an Ardenne (Brabançon), nor every pig into a Yorkshire. Such a result may be obtained by aid of intelligent selection, only when a given race already contains in its "blood" the requisite characters.

This circumstance was perceived by Darwin. "Man can never act by selection, excepting on variations which are first given to him in some slight degree by

[1] For wheat, see Flaksberger, 1915, p. 16.

nature. No man would ever try to make a fan-tail till he saw a pigeon with a tail developed in some slight degree in an unusual manner, or a pouter till he saw a pigeon with a crop of somewhat unusual size; and the more abnormal or unusual any character was when it first appeared, the more likely it would be to catch his attention. But to use such an expression as trying to make a fan-tail, is, I have no doubt, in most cases, utterly incorrect. The man who first selected a pigeon with a slightly larger tail, never dreamed what the descendants of that pigeon would become through long-continued, partly unconscious and partly methodical, selection." ("Origin of Species," chap. i, p. 28.)

At poultry shows in England it was ordered that the comb of the Spanish cock should be upright, and, in consequence, in the course of some four or five years a number of specimens with erect combs were reared; it was then announced that the Polish cock should have no comb or wattles, and the requisite form was soon obtained. "But in all cases," Darwin adds ("Variation of Animals and Plants," chap. xx, p. 198), "the judges order only what *is occasionally produced and what can be improved and rendered constant by selection.*" In other words, characters already present and being *capable of becoming fixed* may be made permanent through selection. But this undeniable statement only shows that in the cases mentioned selection could not create anything new.

It has, for instance, been said of English breeders that they had "created" the thoroughbred horse and the contemporary domestic pig. True, they have produced new types, but, as Bogdanov remarks (1913, p. 10), from such excellent material as the Arabian horse and the Chinese pig, without which they could have accomplished nothing.

In so-called "artificial selection" the new is obtained either (and that chiefly) through hybridisation, by means of spontaneous variations (mutations), or by the selection by producers from stock endowed with a tendency towards exhibiting the required character, or else by means of selecting from mixed material the possessors of an already developed variation. Finally, artificial conditions, favour-

able to the individual and to the further development of present tendencies, may be created.

Pearl (1917, p. 79) quotes Colville (1915), who had endeavoured to improve the American swamp blueberry (*Vaccinium corymbosum*): "seedling plants, even from the largest-berried wild parents, produce small berries as often as large ones." Another case relates to bantams. Pearl (1917, pp. 82-83) referring to his experiments, as also to much information supplied by his correspondents, and to the testimony of the most competent authority on bantams, Mr. Entwistle, affirms that by no selection, unless intercrossing be resorted to, can a small-sized breed of poultry be derived from a large-sized one. Jordan repeats a pertinent epigram of horticulturists, "The first condition for raising a new variety is to have it."

The well-known Belgian fruit-grower, van Mons, in referring to the cultivation of apples, says that new breeds are not created by man; only nature can do that. Shape, flavour, colour, aroma and other characters valuable to man are the products of nature; only the pulpiness and size of fruit are added to by man. All the diversity in the contemporary cultivated breeds of apples, adds de Vries, already existed in the shape of the wild elementary species of apples, although in forms that required improvement. I may add also that in forests on the slopes of the Fergana Range (Russian Turkestan), a striking diversity of forms of wild plums (*Prunus divaricata*, *Pr. ulmifolia*), wild apricots (*Pr. armeniaca*), and wild apples are growing.

The breeder Rümker sharply distinguishes two aspects of methodical selection: (1) the production of new forms, and (2) the improvement of the race. As regards the former, new forms arise spontaneously without the assistance of man; they must be found and then kept isolated (*i.e.* they must not be allowed to cross with other forms), and their progeny will then at once give a durable, pure race. The latter aspect, improving, is man's business; and here, as nothing new can be produced, it only remains to develop what has come to hand.

We may illustrate the foregoing by one more example.

The Andalusian "blue" poultry is a hybrid between black fowl and white with black spots (splashed white). In the progeny of the blue birds the blue, black and splashed white individuals always occur in the proportion of 2 : 1 : 1. The blue fowls are heterozygous. By no selection can the blue colour be fixed; that is, in no case can the blue fowls be made to produce blue fowls only, as in the crossing of the black with the black and the splashed white with the splashed white, when constant forms are produced. In crossing the blue with the blue, besides the blue, black and splashed-white individuals are invariably produced; exclusively blue forms can be obtained only by crossing the black and the splashed-white birds. A constant blue form, says Bateson, could arise only if the gametes of the animal had acquired a "blue factor." But, of course, no selection is able to accomplish that.

4. Selection is thus able to segregate pure lines from mixed material. The importance of selection for keeping the standard of species true will be discussed later (§ 9). But yet another function belongs to selection: it is, as has been observed by Danilevsky (pt. ii, p. 135), the distribution of organisms over the face of the earth. Individuals unsuitable to a given environment are either removed to other places or exterminated.

Let us now present a few cases of the "geographical" action of natural selection. Recent researches have established that the wild ancestor of all the two-rowed barleys (*Hordeum distichum*), although itself a winter form, is less able to resist the injurious effects of frost than are any of the cultivated forms of barley (and even than some spring forms). In regions with a mild winter, the cultivated barleys that have turned wild not infrequently grow together with and amongst the wild forms. Let us suppose that the mean winter temperature decreased; in that case the wild barley would disappear, and its place would be taken by the earlier cultivated two-rowed and six-rowed barleys grown wild (Regel, 1912, p. 513; 1917, pp. 177-178). But in this case

it is self-evident that natural selection could have no influence in *the production* of the forms of cultivated barleys : the latter had already been formed.

In the years of the failure of the oat crop, the wild oat grass *Avena fatua* multiplies in the fields in its stead. In Switzerland the bearded wheat of the Galland variety is being supplanted by the beardless breeds, which are more frost-resistant and ripen more rapidly. The same occurs in Germany in the case of the English bearded wheat of the Rivett variety, etc.[1] But the competing forms themselves, be they species or elementary species, were in existence before selection had assumed its sway.

Sapegin (1922)[2] made the following experiment at the Odessa Experimental Breeding Station. Seeds of pure lines of four varieties of wheat—*lutescens, milturum, erythrospermum* and *murciense* (the first three of which belong to the soft wheats, *Triticum vulgare,* the last to the hard, *Triticum durum*)—were mixed up together in equal quantities. Every succeeding year the seeds of these lines were sown in the proportion obtained at the preceding harvest. As a result of the experiments of four years the hard wheat, var. *murciense,* was all but completely supplanted by the soft wheats, as may be seen from the following table :

PERCENTAGE OF TOTAL QUANTITY OF SEEDS.

Years.	lutescens.	milturum.	erythrospermum.	murciense.
1914	25	25	25	25
1915	33	21	30	16
1916	41·5	27·8	26	4·7
1917	48	27·6	22·5	1·9

The rôle of natural selection is clearly shown here.

[1] De Vries, 1906, p. 62.

[2] Preliminary account of the Odessa Experimental Breeding Station for the ten years 1912-22, Odessa, 1922.

A similar experiment with wheat was made by Pissarev (1923, p. 69) in Siberia, at the Tulun Experimental Station, Government of Irkutsk. During five years were annually sown unsorted seeds of that plant obtained from previous harvests. At the end of that period the resulting crop, in which the beardless white-eared variety originally (1913) predominated, was transformed (1917) into a more uniform aggregate with a marked predominance of the bearded red-eared form :

	Per cent.				
	1913	1914	1915	1916	1917
Triticum vulgare :					
var. *lutescens* - -	72·0	38·8	31·0	23·2	7·6
var. *ferrugineum* - -	10·9	36·5	41·0	49·4	82·4
var. *erythrospermum* -	9·3	13·0	18·4	18·0	5·7
var. *milturum* - -	6·1	11·7	9·6	9·5	4·3
Triticum durum and *Tr. compactum* - -	1·7	0·0	0·0	0·0	0·0

Thus the prevalent form in 1913 was var. *lutescens* (a soft wheat, red-grained, white-eared, beardless), while in 1917 it was var. *ferrugineum* (also a soft wheat and red-grained, but red-eared and bearded).

The struggle for existence and natural selection, says de Vries (1906, p. 71), have assisted in the distribution of elementary species, but there are no grounds for assuming that by these means forms have varied, and that these forms at present possess other properties than they were endowed with from the beginning.

9. IS SURVIVAL A PRIVILEGE OF THE BEARERS OF USEFUL CHARACTERS ?

According to the theory of natural selection, surviving individuals should differ by some useful characters from those which have succumbed in the struggle for existence. On this matter but few experimental researches have been made, and they give results which are not fully convincing.

Weldon carried out observations on the mortality of Carcinus in artificial conditions, but they were conducted in such a way as to throw doubt on his conclusions (see Przibram, 1910, on the subject). On the observations of Bumpus regarding sparrows, and of Crampton on the pupae of the moth *Philosamia cynthia*, we shall have occasion to speak later (chap. x, § 1). We might also mention here the observations of Poulton and Sanders (1909) on Vanessa, by Cesnola (1909) on Mantis, and Harris (1912) on Phaseolus. In all the cases named, it appeared that the surviving individuals differed more or less from those which perished. But other investigations give contrary results. Weldon (1901, 1904) working on Clausilia, Cesnola (1907) on Helix, Kellog and Bell (1904) on the beetle Hippodamia, and Pearl (1911) on chickens, could not observe any perceptible difference between the individuals which survived and those which perished.

As far as may be judged from the available data, *natural selection cuts off deviations from the standard by destroying extreme variations.*

In 2269 capsules of the wild poppy (*Papaver rhoeas*) examined by K. Pearson (1900, p. 383), from 5 to 16, more often 9 to 11, stigmatic bands occur on one capsule. And it thus appears that the capsules in which the number of bands approaches the modal quantity (*i.e.* 10) produce many more seeds than those which differ from the typical form (p. 144). The same proved to be true of the Shirley poppy (a garden variety of the wild Indian poppy), as also of *Nigella hispanica.* In the last-named plant, the standard is eight segments to the seed capsule ; such capsules were the most prolific ; the abnormal ones, as in the poppy, contained but a small number of seeds. (In the cases of both poppy and Nigella, deformed and abnormal capsules were absolutely or relatively sterile.) Hence Pearson (p. 445) infers that " fertility is not uniformly distributed among all individuals, but for stable races there is a strong tendency for the characters of maximum fertility to become one with

the character which is the type. Thus any race as we find it is very largely the product of its modal members; its variability is not the potential variability of the race, but deviates from this maximum limit towards the minimum variability, *i.e.* that of the progeny of a modal mating."

According to the observations of Bumpus (1899), the sparrows that had perished in a storm all deviated from the normal, typical standard (mode) of the sparrows of the locality: those alone had survived which were in possession of wings, tails, etc., of an *average* length.

All the foregoing renders it douhtful whether mortality in natural conditions possesses selective value, *i.e.* contributary to evolution: as a rule, individuals approaching the standard (mode) survive, and all those which deviate therefrom perish, no matter whether their distinguishing characters are retrogressions, or give promise of being able to advance. Selection in natural conditions thus not only does not assist evolution, but appears, in fact, to be a hindrance thereto. Such an opinion was held hy Korshinsky:—"The struggle for existence, and selection connected with it, is an agency tending to restrict the development of forms already produced by checking further variations, but never contributing to the production of new forms. It is a principle antagonistic to evolution" (1899, p. 263). We may further point out that domestic animals and cultivated plants are placed by man in such conditions that the sphere of the application of natural selection is here very limited; in consequence of this the standard cannot be maintained, and indeed we see that these organisms vary very widely.

All who have survived a famine or the ravages of cholera, small-pox, typhoid or plague, are not necessarily the strongest, the healthiest or the most intelligent, as Kropotkin very justly remarks in his book "Mutual Aid, a Factor in Evolution." To this we may add that those who have survived a famine or an epidemic in no measure transmit to their

descendants immunity from the hardships experienced or from the disease they were attacked by. The reverse is the case, as an enfeebled constitution is generally transmitted. Those who possess congenital immunity, say from small-pox, transmit it to their posterity, and it is then quite immaterial whether the individual had small-pox or not, *i.e.* whether or not he had undergone (in the given case) the vicissitudes of the struggle for existence.

The opinion of Chernyshevsky on the effects of the struggle for existence closely corresponds to the above-stated views of Kropotkin. In natural selection, says Chernyshevsky (p. 35), all animals are subject to the same process, which results in the destruction of a certain number. "The most usual form of natural selection is the extinction of superfluous beings from want of food. In such a case is it only the dying beings which are exposed to hunger? No, all are equally exposed to the risk. Does the farmer act in this way in relation to his herd? Would his herd improve if he hindered reproduction by exposing all his animals to hunger? The surviving animals would be weakened and injured, and the herd would deteriorate." While killing his inferior stock by blows on the head, the farmer does not apply this method to the cows he would wish to preserve. And yet natural selection operates in precisely this way.

In short, artificial and natural selection, as we have had occasion to show, are two very different things. In the first operates the intelligent will of man, in the second blind chance. Man, engaged in the improvement of his breed in a rational manner, crosses *only* what is useful, selecting from the offspring *only* the useful, removing *all* else. Nature can do nothing of the kind: it is extremely unlikely that just those individuals which accidentally possess a useful variation should intercross. The probability of such a contingency arising would considerably increase, if the number of individuals exhibiting such a variation was great (say, half of the total population); but with such an assumption the very principle of chance and selection becomes superfluous; new characters

therefore arise in accordance with a certain law. According to Darwin, a useful variation appears in an insignificant number of individuals. If chance brings together two individuals with useful variations, it may happen as often as not that their progeny will perish, while the comparatively worthless material will survive and multiply.

All processes in inorganic nature finally lead to the most stable condition, which is likewise the most probable. Therefore, in the "struggle" which takes place in the midst of inorganic nature between chemical elements of various forms of energy, the most stable element takes the upper hand: unstable radium is transformed into other more constant, more durable substances (helium), undulatory is transmuted into the less regular, thermal vibration.[1] And yet in the organic world the principle of the greatest stability coincides with the idea of fitness, although fitness is of all events the least probable. Life is, therefore, the accomplishment of a certain process, which, from the standpoint of physics, is of the smallest order of probability.[2]

This line of thought is not far removed from that followed by K. E. Baer. Darwinians, he says (1873, p. 12), reason thus: what survives in the struggle for life is thereby fit. But in every contest, retorts Baer, success belongs not to the fit, but to the tough (most durable—das Dauerhafte): dwellings cut out of the rock are the most durable, but nobody would call them the most fit for habitation.

It has already been observed that the principle of the *survival of the fittest* expresses a self-evident truth, for the fittest is the best adapted for life; and therefore the survival of the fittest means the survival of whosoever can survive. The whole problem is reduced to the determination of the means by which the adapted organism obtains the characters which enable it to survive.

[1] It was formerly assumed that heat is an entirely irregular motion. But recently it has appeared that this is not quite the case.

[2] See on this point my book, "Theories of Evolution," Petrograd, 1922, chap. i (in Russian).

10. THE COURSE OF EVOLUTION

Also bestimmt die Gestalt die Lebensweise des Thieres,
Und die Weise zu leben, sie wirkt auf alle Gestalten
Mächtig zurück.

GOETHE, "Metamorphose der Thiere."

We regard the morphological and physiological characters of organisms as a manifestation of the chemical structure of their plasm, or, better, as a resultant of the chemical structure of their albumens. If we knew more fully the chemical nature of organisms, we might then be able to make use of the chemical structure of their albumens as diagnostic characters, instead of characterising them by means of stamens, antennae, scales, etc. Specific distinction (or, more generally, distinctions between any forms) are primarily rooted in the stereochemical combination of the molecules of their albumens or, generally, of the substances of which organisms are composed.

Let us give three instances. According to the investigations of S. Ivanov (1917) the oils of fungi and algae differ from those of the higher plants. The oils of the lower plants are composed of saturated acids; of non-saturated they possess only those of the type of olein ($C_{18}H_{34}O_2$) and linol ($C_{18}H_{32}O_2$) acids, while linolen ($C_{18}H_{30}O_2$) acid, which is in the highest degree non-saturated, is absent. This last type appears only in conifers (as also in higher plants). A strict correspondence between the systematic position of the species and the chemical composition of its oil generally occurs, and the natural system of its oils fully corresponds with that of the vegetable kingdom. It is thus possible to speak of the oils of Cruciferae, Malvaceae, Lycopodiaceae, etc. From experiments made on the blood-serum of the Dutch, Chinese, Javanese and Malays, carried out by Bruck (1907), it appears that Europeans (for instance, the Dutch) possess a more complex structure of the protein molecule than do the lower races. Reichert has shown that haemoglobin in animals and starch in plants are specific for every species.

From such a point of view, inheritance consists in the transmission from parents to children not of morphological elements or of any particular hereditary substance, but of a certain combination of molecules ; such a combination, or structure of the albumen, enables the children to respond in similar circumstances to stimuli in the same manner as did *their parents, and in* conformity *thereto to reproduce similar forms. As was shown in 1894 by E. Fischer, every* ferment may operate on that body alone which possesses a *very similar molecular structure. Even metallic colloids* interact if they are stereoisomerical. As life is inconceivable without fermentative processes, it is clear that ferments act identically only when the stereochemical combination of the molecules of the albumens upon which the ferments operate, are also like.

In this lies the secret of heredity. The capacity for like metabolic processes, according to Ruzicka (1909), is inherited. As is justly observed by Rable (1905), stability in the phenomena of heredity is the attribute not of matter, which changes constantly, but of the *capacity* to transform external stereochemical complexes into complexes characteristic of a particular biological structure ; or, in other words, the capacity for uniform assimilation and metabolism. Fick (1907) defines heredity as a *capacity* of live albumens to elaborate the same stereochemical combinations of atoms as were possessed by the ancestors of the given individual—the direct transmission of separate molecules by parents to children, or the inheritance of such, never taking place.

Effects experienced by the organism in the process of evolution are of two kinds : the first are lodged in its own organisation and in the chemical properties of its albumens, and do not depend on external conditions. Such causes we call *autonomic*. The second kind of influences proceed from the environment, from the entire complex of the medium or the surrounding living and inanimate nature,—in a word, from the geographical landscape (in the widest meaning of

the term). To these influences we give the name *choronomic* (from the Greek word *choros*, signifying place, region), or they may be called *geographical* in the narrow meaning of the word. A fuller demonstration of the foregoing will be presented in the subsequent chapters of this book.

The outcome of evolution is a certain mean resultant of autonomic influences on the one hand, and of geographical *(or choronomic) on the other. These two causes are the* major laws which regulate the development of the organic world. A one-sided activity of one of these factors may easily drive the organism into such a position as may cause its ruin.

We may here remark that Eimer (1897, p. i, p. 15) refers the cause of transmutation primarily to the influence of external conditions; to the use and disuse of organs he attributes a secondary importance; and natural selection he relegates to the third place.[1] The inner causes, in his opinion, play the part of an agency that hinders variability "*in* all directions." The inadequacy of such an estimate of the value of internal causes will be demonstrated in one of the following chapters.

R. E. Regel (1917), *on the contrary*, is disposed to deny the importance of physico-geographical conditions in the production of species. This opinion of Regel's is based on the circumstance that the contemporary theory of genes, or factors, very satisfactorily explains the processes of the formation of recent species by means of a recombination of *already existing* hereditary genes, whereas "it completely fails to indicate the path followed in the evolution of organisms by progressive development, which ever demands the occurrence of something absolutely *new*" (p. 179).

Our point of view attributes importance to the inner and to the external (geographical) agencies.

[1] "The aspect of the organic world is produced by external effects, and its continuous existence is only due to the unceasing activity of these influences" (*Eimer*, p. 16).

Natural selection, as may be seen from the foregoing, has in our opinion no importance in the evolutionary process, *i.e.* in the production of new forms. How does the case stand with the *extinction* of organisms? In Darwin's opinion ("Origin of Species," chap. xiv) the extinction of species and of whole groups of species which has played so conspicuous a part in the history of the organic world, almost inevitably follows from the principle of natural selection; for old forms are supplanted by new and improved forms.

In our opinion, just as evolution depends upon inner (autonomic) and external (geographical) causes, so is extinction due to the same two causes.[1]

Every group of organisms in the course of a definite period attains its optimum, after which, obeying certain internal impulses concealed in the constitution of the organism,[2] it becomes extinct or is relegated to a secondary position, yielding its place to others. Thus in the Mesozoic era gymnosperms prevailed, while in the Upper Cretaceous and Tertiary they yielded their place to the angiosperms. Reptiles flourished in the Mesozoic, and mammals in the Tertiary era. In this process the struggle for existence usually plays no part.[3]

Similarly, every organism dies its natural death when, according to its organisation, the time allotted to it by Nature has expired; some insects live only a few hours, whereas, independently of the struggle for existence, the cypress and the yew attain an age of three thousand years.

To the number of external causes that may lead to extinction belong change of climate, soil, and vegetation, transgressions and regressions of seas, contagious diseases

[1] On the causes of extinction various opinions have been held. See Neumayr (1889), Steinmann (1908, fantastic!), Osborn (1910, pp. 172-176, 500-509), R. Hörnes (1912), Depéret (1915), Kulagin (1919).

[2] These inner causes will be more fully treated of in the concluding part of chap. iii.

[3] I say *usually*, for when from internal causes the numbers of a species diminish, the struggle for existence may contribute its quota to the final extinction.

and other forms *of the extermination of some organisms* by others. As may be seen, the struggle for existence also plays some part, although indirect, in the disappearance of organisms from the earth's surface. We must not lose sight of the fact that geographical (external) causes assist in the extermination of given forms only when this is so predetermined by internal agencies.

As will be more fully exposed later, the arising of forms one from another is subject to certain laws, and proceeds in a determined direction; it is not due to the vagaries of chance. Some of these laws we know, such as those discovered by Mendel to which combinations of hereditary units are subject, the chemical correlations of organs due to internal secretion, the sequence and order exhibited in embryology and palaeontology in the development of organisms. But in what manner the combination of all these and many other causes leads to the production of definite organic forms as yet remains a mystery. What cause *induces an organism to vary in a determined direction* is still concealed from us.

A certain influence belongs to external agencies, *i.e.* to the environment or geographical landscape. But it is remarkable that the organism possesses the capacity for adapting itself to the environment in an active manner. It thereby reveals the presence, as it were, of a certain regulating prineiple ; while on the other hand, through the effects of internal constitutional causes, which depend on the chemical structure of the protoplasm, development proceeds in a determined direction in defiance of external conditions.

The *casting vote in the question of the course and causes* of evolution belongs to palaeontology. And it is noteworthy that the most competent authorities in that branch of science are adverse to the principle of the struggle for existence. In illustration we may mention Cope, Marsh, Osborn, Zittel, Depéret. Osborn (1912, pp. 277-278) says

that new characters arise through the operation of an unknown law, *but not by chance* ("*there is an unknown law operating in the genesis of many new characters and entirely distinct from any form of indirect law which would spring out of the selection of the lawful from the lawless*," p. 277), and quotes the words of Aristotle, "Nature produces such things, which being impelled by a certain principle confined within them, attain a determined end."

Ontogeny, says the American palaeontologist (p. 278), is a process which cannot be conceived by the human mind: we are unable to understand how an insignificant germ of fertilised organic matter can be transformed into a gigantic whale or dinosaur. The whole process of ontogeny may, of course, be traced out in the minutest details, but we do not thereby approach a step nearer towards the solution of our problem. Phylogeny may possibly be a puzzle of the same kind. The only thing we can do is to trace out the manner in which new characters arise, the immediate causes remaining hidden from us.

CHAPTER II

PHYLOGENETIC ACCELERATION, OR THE PRECESSION OF PHYLOGENY BY ONTOGENY

One of the most striking arguments in favour of development operating in a determined direction without the intervention of chance, is afforded by the interesting phenomenon of the precession of characters, or phylogenetic acceleration.

By the term *precession of characters* we understand the following series of phenomena :

(1) *Palaeontology* teaches us that in young forms characters not infrequently occur which, while disappearing with advancing age, reappear in more recent geological deposits both in the young and in the adult. In their development the young seem to be pushing ahead of their time.

(2) From the study of *embryology* we may gather that the larvae not infrequently possess morphological and physiological *characters of a higher organisation, which vanish in* the adult state. The adult thus seem to lag behind the young stages of their development.

(3) *Comparative anatomy* reveals the occurrence, in the more lowly organised groups, of characters which are peculiar to groups standing higher in the system. It often happens that in tracing the palaeontological evolution of a group we observe that characters belonging to it already occurred in a lower group before the higher one came into existence: as, for instance, in the case of some Palaeozoic organism which is beginning to shadow

forth what will in time be fully developed in those of the Mesozoic era.

The precession of characters may thus be observed to occur in the development of both the individual (ontogeny) and of entire groups (phylogeny).

A. *PRECESSION IN ONTOGENY*

1. PALAEONTOLOGY

A. P. Pavlov (1901), in his work on the Lower Cretaceous ammonites, called attention to the following :—*the young of certain ammonites possess characters which disappear in the adult state, while the same characters subsequently reappear in the more highly organised representatives of the same group belonging to species that occur in more recent geological strata.* The young precursors, coming before their time, foreshadow what will subsequently be displayed in adults.

This fact is antagonistic to the " biogenetic " law, according to which an organism in its individual development is supposed to reproduce the stages that have been passed through by the species in its phylogenetic development (" ontogeny recapitulates phylogeny "). In the phenomenon of which we shall now speak, ontogeny, as it were, *anticipates* phylogeny.

In the Lower Kelloway ammonite Kepplerites the inner (younger) whorls very much resemble those of an adult Cosmoceras of the *jason* group. It would seem that Kepplerites passes through the stages of development of Cosmoceras, and that the former is derived from the Cosmoceras of the *jason* group. But that cannot be the case, as Kepplerites is *older* than Cosmoceras of the *jason* group : the first is peculiar to the Lower, the second to the Middle Kelloway (Pavlov, p. 62). The young of Kepplerites thus anticipates, as it were, the forms of future ammonites. This phenomenon has been called by Pavlov the prophetic phase.

Let us take another example. The young of the ammonite *Simbirskites elatus*, 25 mm. in diameter, very much resembles the adult of *Simbirskites decheni* with a diameter of 50-60 mm. It would seem that *S. elatus* was derived from *S. decheni*; but such is not the case, as *S. elatus* is geologically older than *S. decheni*. Here again we have a case of precession of characters or phylogenetic acceleration. The same phenomenon is exemplified, according to Pavlov, in belemnites, Turritella and the milk dentition of the Equidae: the anterior molars in the milk dentition of the ancestors of the horse are always more complex than the permanent teeth; they thus anticipate the forms of teeth that will hereafter appear (p. 64).

The phenomenon of phylogenetic acceleration, just described, may be explained by the given organism possessing latent characters (factors, *genes*) originally manifested in the young alone, which factors in the course of time and evolution are displayed also in the adult descendants (or supposed descendants) of that organism.

2. ONTOGENY

Rhumbler (1897) offers several instances of the ontogeny of the shell of the Foraminifera following a course opposite to that which it would be expected to take by the so-called biogenetic law, and developing in the direction "from a higher to a lower condition." The imperforate foraminiferous *Peneroplis pertusus*, of the Miliolidae, possesses a very finely perforated embryonic chamber, whereas all the remaining part of the shell, *i.e.* all the chambers that succeed the embryonic one, bear no true pores; in certain cases only may be observed small pits sinking into the wall of the shell from the exterior and ending blindly. Here features of a higher organisation are met with in the first chamber (in the young animal), while they are absent in all the succeeding chambers, *i.e.* in the older animal. That the presence of pores is a feature of a higher organisation may be seen from the following. The

first chamber of the shell in nearly all perforate Polythalamia possesses relatively much fewer pores than occur in the walls of the succeeding chambers ; sometimes the pores in the first chambers are entirely absent, or are much smaller than in the chambers of the growing end. Among the fossil Foraminifera, says Rhumbler (p. 170), no instance can be encountered of a perforate having developed into an imperforate one, or a densely into a scantily perforated shell wall. On the contrary, the opposite is observed to occur in the evolution of the Foraminifera, the perforate being derived from the imperforate forms, and a dense from a sparse net of perforations.

Other instances of the above may be given. Thus, the primordial end of the foraminifer Trochammina is spirally twisted, whereas the growing end is straight. The chambers of the primordial end of the polythalamous *Bigenerina patula* are arranged in two rows, while those of the growing end are disposed in one. It can be demonstrated palaeontologically that the primordial chambers of these forms are constructed on a higher plan. The first chambers of the shells of many Nodosariidae are decorated with protuberances, ribs or spines, whereas the succeeding chambers are devoid of such a sculpture.[1]

In all such features Rhumbler (p. 188) sees a manifestation of " the law of the great independence in the variations of the separate stages of development of the Foraminifera." He regards all the peculiar characters of young Foraminifera as being purposive, and accounts for them by the conditions of life, which demand a greater solidity of the shell.

One of the most striking examples of phylogenetic acceleration is the presence in the larvae of ascidians of features by which the vertebrate embryo is distinguished : the notochord, the dorsal nervous system, the otocyst, the ocellus (with a retina, pigment layer, lens and cornea) and the gill-slits. In the adult Tunicata most of these characters disappear.

[1] Compare also Rhumbler, 1911, pp. 32-37.

Some myriapods, such as the Chilopoda, to which the centipede Geophilus and others belong, hatch from the egg with their full complement of legs. But in Scolopendrella, Pauropus, several representatives of the Diplopoda, including Julus, Glomeris, Polydesmus and others, the embryo hatches from the egg in the shape of a larva possessing only *three pairs of legs, like adult insects.* The remaining legs are altogether absent (as in Polydesmus, Strongylosoma) or rudimentary (Glomeris). As development proceeds new legs appear in the six-legged larva in the posterior part of its body, and it gradually assumes the shape of an adult myriapod.

Larvae of some Diptera have a nervous system which is more highly organised than is that of the imago. Thus in the larva of the fly Stratiomys all the ganglia are fused into one central nervous ganglion, while in the adult state five ventral ganglia are observed, *i.e.* a more primitive condition.

In the fore-brain of both mammals and birds in the region of the foramen of Monro there is a structure called the hippocampus, or cornu ammonis. A rudiment of it is found in reptiles. Thus in the embryo of the lizard Anguis the brain in the region of hippocampus very much resembles the corresponding region in the embryo of Ornithorhynchus : in both a median thickening, eminentia medialis, occurs, from which the hippocampus subsequently arises in Ornithorhynchus. However, in the lizard the thickening does not further develop, but flattens out in the course of time, so that the median wall of the hemispheres is perceptibly depressed in the adult (Kupffer, 1906, p. 238). In the embryo of the lizard we thus find the rudiment of an organ that becomes reduced in the adult, but reappears in the more highly organised birds and mammals. True, the hippocampus is found in the dipnoan fishes, and amongst the amphibians in the Gymnophiona; but both these groups are lateral branches, with which reptiles have nothing in

common, and even if they had, it would not affect the argument.

As is generally known, in the lower vertebrates (Anamnia) all the divisions of the brain lie in one plane ; in all the Amniota, on the other hand, the brain forms a series of curves. In mammals, where these latter are more prominently expressed, we may observe the parietal curve, the pons varolii curve and the occipital curve. It is remarkable *that these curves are manifested in the embryos of all the* Anamnia, while in the adults they disappear.

The young of the anthropoid apes in many respects resemble man more closely than do the adult animals. A straight femur is one of the most prominent peculiarities of the genus Homo, yet in young gibbons, chimpanzees, and in some South American monkeys, the femur is straighter in comparison not only with that of the adult forms of the same species, but even with that of man (Klaatsch). In all young mammals the capacity of the skull is relatively greater than in the adult state, but this circumstance is especially striking in the case of anthropoid apes.

As will be more fully discussed later, we regard the monocotyledons and the dicotyledons as two parallel branches which have developed independently. But the latter have advanced further in development. According to Miss Sargant (1903, 1908), the principal distinction (though not always present) is that the stem of the dicotyledons possesses an active cambium while the monocotyledonous stem does not. In connection with this circumstance, the fibrovascular bundles in the dicotyledons are arranged in a circle, while in the monocotyledons they are disposed without order. *But it is remarkable that in the first internodes* of the young seedlings of the monocotyledons may be observed, according to Miss Sargant, hints of the structure of dicotyledons, namely, a disposition of the conducting bundles in a circle, their collateral structure, and traces of cambium. Thus, traces of a transitory cambium have been observed in

the seedlings of the yucca, banana, Dracaena, Typha, lily, *Fritillaria*, Gloriosa, maize (see Lotsy, 1911, p. 618). In the course of the subsequent development this disappears and the stem acquires the structure typical of monocotyledons. Those who derive the monocotyledons from the dicotyledons see here a case of the recapitulation of phylogeny by ontogeny. Regarding monocotyledons as a branch independent of dicotyledons, we consider the peculiarities noted above as a case of phylogenetic acceleration, *i.e.* as a tendency towards developing the structure characteristic of forms that have advanced further in their evolution.

3. DIVERGENCE IN THE YOUNG AND CONVERGENCE IN THE ADULTS

The young of a species generally differ less from the young of a nearly allied species, than do the adult forms of the same species one from another (and the embryos of even very remote forms are sometimes, as is well known, indistinguishable). But the reverse sometimes happens. In the Siberian seas is very widely distributed the isopod *Chiridotea sibirica* (Birula, 1896). The common brackish and fresh-water *Ch. entomon* (L.), allied to *Ch. sibirica* and occurring near the coasts of the Arctic Ocean, the Baltic, in the lakes of Ladoga, Mälar, Wetter and other fresh-water lakes, as also in the Caspian Sea, has been derived, according to Ekman (1919, p. 503) from *Ch. sibirica*, by being gradually adapted to live in brackish and fresh water. But it is remarkable that the young of *Ch. entomon* differs more from the young of *Ch. sibirica* than do the adult forms of these species one from the other. The same is true of another species of the same genus, *Ch. sabini*: the young *Ch. sabini* differs much more conspicuously than the adult from the adult *Ch. sibirica* and *Ch. entomon*. Furthermore, *Ch. megalura* is a deep sea form very nearly allied to the shore form *Ch. sabini*, and to all appearances has been derived from it. Yet it appears that the young of these

two forms differ more markedly from one another than does adult *Ch. megulura* from *Ch. sabini* (Ekman, 1919, pp. 508-511).

Rana tigrina and *R. cancrivora*, both from India, are so closely allied that the latter was regarded as a variety of the former; yet their tadpoles differ widely in the structure of the mouth (Boulenger and Annandale, 1918). A. N. Kirichenko has kindly drawn my attention to the fact that while the imagos of the several species of the moth Cucullia, of the *C. verbasci* type, are scarcely distinguishable, their caterpillars differ sharply one from another. Similar instances are furnished by Peter (1920, p. 76) in the case of the moths Acronycta, Deilephila, Somabrachys. The well-known hymenopterologist, Konow, regarded the two tenthredinids, *Lophyrus pini* L. and *L. similis* Ntg., as belonging to one species; and yet the two are well distinguished by the colour and habits of their larvae. *Chermes strobilobius* Kalt. and *Ch. lapponicus* Chol. were formerly regarded as one species, but their life-cycle is not the same, nor are their larvae, hatched from the eggs deposited by the winged females. The winged females of *Ch. strobilobius*, emerging from the galls of the spruce (Picea), migrate to the larch and deposit their eggs on its leaves, from which larvae with relatively short bristles on the proboscis are hatched; the winged females of the *Ch. lapponicus* emerging from the galls of the spruce, on the contrary, deposit their eggs *on the same tree* (not the larch); from these eggs larvae with very long bristles on the proboscis are hatched. Cholodkovsky (1910) accounts for the difference in the length of the oral bristles in the following way: the larvae which are destined to suck through the thick bark of the shoots of the spruce possess long suctorial bristles, while those which are obliged to negotiate the thinner bark of the larch have shorter bristles.

B. ACCELERATION OBSERVED IN PHYLOGENY.

In this section we shall consider the occurrence of characters of higher forms, not only in the embryos or larvae, but also in the adult of the lower forms,—in a word, *all cases in*

which the organism, no matter whether adult or immature, is in advance of its time or of the average level of its companions in the group. Every now and then it may be observed that lowly organised plants or animals possess one or several characters of a superior degree of specialisation, characters which are displayed only by organisms holding an incomparably higher position in the system or occurring in more recent strata.

Let us begin with the vegetable kingdom.[1]

1. PLANTS

1. One of the most remarkable examples of phylogenetic acceleration is afforded by the BENNETTITALES, an extinct group of gymnosperms peculiar to the Triassic, Jurassic and Cretaceous systems. They are often grouped together with the Cycadales, to which they bear an external resemblance, but they undoubtedly constitute a separate class, not connected directly with the Cycadales.[2]

The Bennettitales show many points of resemblance with the angiosperms, possessing at the same time much more primitive characters than the now existing Cycadales, and thereby approximating to ferns. Let us first examine the features exhibiting a superior organisation.

The reproductive organs of the Bennettitales are assembled into peculiar cones, or strobili, carrying both the male organs, or microsporophylls, and the female, or megasporophylls. The " cone," or in the terminology of Arber and Parker, the anthostrobile of the Bennettitales, very distinct from the cone of the Cycadales, exhibits a certain resemblance to the flower of the angiosperms. While the cone of the Cycadales (as in Zamia, where the female organs are likewise gathered together in a cone) is a unisexual organ, the anthostrobile of the Bennettitales is a bisexual one. Similarly to what occurs in bisexual flowering plants, the female organs in the Bennettitales

[1] See also chap. iv on " Convergence."

[2] The phylum of gymnosperms is at present divided into the following seven classes: (1) Pteridospermae or Cycadofilices, (2) Cycadales, (3) Bennettitales, (4) Cordaitales, (5) Gingkoideae, (6) Coniferae, (7) Gnetales. The classes 1, 3 and 4 are extinct.

are attached nearer to the apex of the cone axis, above the male organs, while at the base of the axis may be seen a floral integument of sterile bracts, corresponding to the perianths of the lower angiosperms. The cone of the Bennettitales is the earliest representative in the vegetable kingdom of the flower with its perianth, androecium and gynoecium.[1]

The bisexuality of the reproductive organs of the Bennettitales is a most remarkable fact, denoting a very high stage of development, as all other gymnosperms (with the sole exception of Welwitschia with its incipient bisexuality, of which more hereafter), both living and fossil, possess unisexual organs of reproduction, bisexuality being a feature of the more highly organised angiosperms. *In the organisation of the ovules* the Bennettitales furthermore hold a very high position, so that in that respect they cannot even be classed with the gymnosperms proper, in the strict meaning of the term. While the ovules of the Cycadales are naked, being attached to the microsporophylls and merely covered by their own integument, each ovule in the Bennettitales is enclosed by several sterile scale-like leaves, which expand at the extremity; these scales, while uniting at their margins, leave uncovered only a very small orifice, through which protrudes the extremity of the ovule's integument with the micropyle. The ovule here is thus completely closed. True, the "pericarp" is formed of sterile scales, not of carpels, and the pollen comes in direct contact *not with the stigma, which is formed from carpels*, but *with the ovule itself*, or, to be more exact, with an excrescence of its integument, as in the Gnetales (in Welwitschia, for instance, for which see below); the Bennettitales possess neither style nor stigma. But, however that may be, the ovule itself remains closed, whereby the same effect is produced, although by different means, as we find in typical angiosperms.

Then, the "flowers" of the Bennettitales are large, attaining 14 cm. in diameter, which also is a feature pertaining to a superior organisation. Finally, the embryo is constituted exactly on the angiosperm type, and the seeds are exalbuminous.

[1] The view according to which the fructifications of the Bennettitales are regarded as inflorescences is no longer tenable.

There are grounds for assuming that the "stamens" in the *Bennettitales* ripened earlier than the female organs, *i.e.* the flowers were protandrous. If that was so, the Bennettitales must have possessed cross-fertilisation, evidently accomplished by means of insects, which visited the flowers, possibly for the sake of the pollen. That would also constitute a feature belonging to a higher organisation; for of all the gymnosperms now living, with the exception of Welwitschia (and of some other Gnetales and some cycads),[1] none are cross-fertilised by insects.

Yet, at the same time, in the Bennettitales are found many features of a lower organisation, much inferior to that of the Cycadales. To such we may in the first place refer the male organs, "stamens," or microsporophylls. They have the appearance of bipinnate structures, outwardly entirely unlike not only the stamens of angiosperms, but even the microsporophylls of the Cycadales, closely resembling on the other hand the sporophylls of ferns. The structure of the microsporophylls of Bennettitales with their microsporangia united into synangia and protected by a thick covering, very much recalls what may be observed in the most lowly organised ferns, such as, for example, the now living Marattia. Moreover, many Bennettitales had, like the ferns, scale-like hairs at the base of the leaves, and into every leaf penetrated only one fibro-vascular bundle from the stem. All the above are characters of a much lower organisation than belongs to the Cycadales, characters which approximate the Bennettitales to ferns. With the Cycadales they share in common only the outward appearance, especially as regards the leaves.

The evidence given above shows that the Bennettitales are very lowly organised gymnosperms, which have in some respects made a very considerable advance in their development, and may be said to imitate the higher angiosperms (which first made their appearance only in Lower Cretaceous time).

We are thus disposed neither to unite the Bennettitales with the Cycadales, as we regard both as two parallel branches, nor to derive the most primitive angiosperms,

[1] In the South African cycad Encephalartos, fertilisation by beetles has been observed (Rattray, 1913; see also Diels, 1916, p. 769).

viz. the Polycarpicae, from them. The resemblance *between the Bennettitales and the angiosperms is the* result of convergence, due to phylogenetic acceleration.[1]

2. Angiosperms, or flowering plants in the narrow meaning of the word,[2] may be characterised by the following features:—the carpels form a pistil with an ovary in *which are enclosed the ovules and a stigma; the ovule* possesses a very rudimentary prothallus, without archegonia, but with a distinct egg-cell in the embryo-sac; the albumen or endosperm appears after fertilisation; the pollen-grain contains one reproductive (nucleus) and one vegetative cell; fertilisation is accomplished by the aid of wind, animals, more rarely water; flowers diclinous or monoclinous; trees, shrubs and grasses (Wettstein, 1911).

The plants belonging to the class of GNETALES, the highest of the gymnosperms, possess a remarkable combination of gymnosperm and angiosperm (anthophyte) characters.

To this class, which is practically unknown in the fossil state,[3] *belong only three genera—the common* Ephedra, the tropical Gnetum and the South African *Welwitschia mirabilis*. Though true gymnosperms, they possess the

[1] We may note that Arber and Parkin (1907) (who have advanced the theory of the origin of the flower from the anthostrobilus of the Bennettitales) and Kuznetzov (*1904*, p. *550*), do not regard the Bennettitales as tho direct ancestors of the angiosperms, both of these being, in their opinion, parallel branches deriving their origin from seed-ferns through the hypothetical Proanthostrobilatae, while the Cycadales constitute a separate branch. Berry (1916, p. 36), the most recent of the authors who have written on the geographical history of the gymnosperms, explicitly asserts that Bennettitales are a side branch, never having given rise to any other.

[2] Wettstein (1911) divides the Anthophyta into two divisions: the gymnosperms and the angiosperms. Kuznetzov (1914, p. 20) does not regard the gymnosperms as Anthophyta, as he considers angiosperms and Anthophyta to be synonymous terms. In view of such a discrepancy, it is better not to use the term Anthophyta, employing instead that of angiosperms, which will lead to no misunderstanding. We may call "*flower*" either an organ provided with an ovary (and in that case the angiosperms alone could be called anthophytes), or an unbranched shoot, restricted in growth and modified in a peculiar manner for the purposes of reproduction (in which case, besides the angiosperms, not only the gymnosperms, and among them the Bennettitales, may be termed anthophytes, but the spike of a horsetail or a club-moss might also be called a flower (Kuznetzov, pp. 8-10, 514). Goebel, indeed (1915-18, p. 1085), speaks of a "flower" in Lycopodium, Selaginella and Equisetum.

[3] Male inflorescences of *Gnetum scandens* have lately (1915) been discovered in the Pliocene beds of Holland (Seward, vol. iv, 1919, p. 470).

following features shared by angiosperms: true vessels in the xylem, male flowers provided with a well-developed perianth, and the female with closed carpels, forming something like an *ovary*, which, as has just been indicated, is peculiar to angiosperms.[1] By these carpels of the female flower *is enclosed the ovule* of the Gnetales, which only just protrudes in the shape of a distinct organ (tubulus), physiologically performing, as it were, the part of a style and stigma by intercepting the pollen, although morphologically it must be regarded as a part of the ovule. The Gnetales, says Kuznetzov (1914, p. 156), may be regarded as half gymnosperms, half angiosperms.

All gymnosperms (with the exception of Bennettitales) and the lower angiosperms are, as is well known, unisexual. Bisexuality in angiosperms is a feature peculiar to a superior organisation. And yet we see in the male flowers of Welwitschia beside the six stamens a rudimentary ovule. True, this ovule is sterile, but it is none the less provided with an integument and a tubule ending in a stigma. We repeat that the ovule and the entire rudimentary female organ of Welwitschia is physiologically functionless; still, speaking morphologically, the flowers of this singular plant are bisexual.

What value can be possessed by this rudiment of a pistil which is of no practical use to the plant? Had it been an inheritance from ancestors, similar to the vestigial organs, of which numbers are known in the comparative anatomy of animals, the matter could be easily accounted for. But here we have the "rudiment" of an organ which will only begin to function in the monoclinous flower of the angiosperms. The male flower of Welwitschia is an excellent illustration of phylogenetic acceleration, or of the foreshadowing by primitive organisms of what will subsequently be embodied in higher forms.[2]

[1] We may here call attention to Kuznetzov's view (p. 167), according to which the integument of the ovule in Gnetales is not the carpel, but the perianth. Even should we agree with this interpretation, which seems to me rather far-fetched, the Gnetales would still possess female flowers supplied with a perianth which is highly organised.

[2] It would be only just, however, to record the opinion of Czelakowsky, according to which, from the presence of a rudimentary ovule in the male flowers of Welwitschia, it may be inferred that the primary gymnosperms possessed monoclinous flowers, from which diclinous flowers have been

In Gnetum the flowers are as a rule dioecious, but in some species (*G. gnemon*) in male inflorescences occur undeveloped female flowers, which possibly serve as nectaries, thereby attracting insects. The species of Ephedra are generally dioecious, but several are sometimes monoecious. Wettstein (1907) has described specimens of *Ephedra campylopoda* from Dalmatia in which, by the side of the exclusively female, monoclinous inflorescences occur: at the extremity of the male inflorescence female "flowers" are attached, which, although forming *normal archegonia, as far as is known, fail to produce fruit.* Wettstein assumes that in this case the *transformation* of diclinous into monoclinous inflorescences may be observed (see Lotsy, pp. 293-295).

To the same class of phenomena may be referred the monoclinism of cones, sometimes (as an exception) to be found in the Conifera—larch, Picea, Sequoia, Pseudotsuga, juniper, etc. Krechetovitch has recently (1921, p. 42) fully studied the monoclinism of cones in the European, Siberian, and Daurian larch.

Let us proceed. The ovule in the gymnosperms has but one integument, while in the choripetalous angiosperms it has usually two. Now, in Ephedra and Welwitschia the ovule possesses one integument, while in Gnetum, as in the choripetalous angiosperms, it has two.[1]

The embryo-sac in Gnetum and Welwitschia is developed according to a type which is intermediate between gymnosperms and angiosperms; in some species of Gnetum the albumen is formed after fertilisation, as in angiosperms, not before, as in gymnosperms. Neither Gnetum nor Welwitschia possesses even rudimentary archegonia, as is the case with other gymnosperms. But in the manner of formation of the female prothallus in the embryo-sac, Welwitschia has retained some traces of its connection

subsequently derived. This suggestion, however, seems to me difficult to substantiate, as in the series of gymnosperms the Gnetales occupy the highest position, and it is hardly probable (although not impossible) that a character peculiar to archaic gymnosperms should occur in the most highly organised representatives of that group. In Wettstein's opinion (1911) there is nothing to support the view of the former occurrence of monoclinism *in contemporary gymnosperms. (See also Lotsy, 1911, p. 294.)*

[1] Kuznetzov (p. 169) supposes, that in Gnetum the outer integument of the ovule, supplied with fibro-vascular bundles, most likely belongs to the perianth.

with the Archegoniata. Yet the embryo-sac in Ephedra develops entirely after the type of gymnosperms: a typical prothallus with archegonia is formed before fertilisation.

Gymnosperms are usually fertilised by the aid of wind, but in Welwitschia the pollen is transferred to the ovule by means of the bug *Odontopus sexpunctatus*. It is supposed that in both Ephedra and Gnetum insects also take part in fertilisation.

Gnetum also approaches the dicotyledons in the reticulate venation of its leaves.

In view of such resemblances with the angiosperms, it may be asked, whether the latter are not derived from the Gnetales. Wettstein (1911) admits that the flower of the angiosperms may be evolved from the inflorescence of the gymnosperms—for instance, of Ephedra; he assumes that if the Gnetales are not the direct ancestors of the anthophytes, they in any case indicate the way in which the transformation of the gymnosperms into the angiosperms may have taken place. Kuznetzov (1914, p. 154), on the contrary, in his remarkable "Introduction to the Classification of the Flowering Plants," regards the Gnetales as "gymnosperms, risen above the level of the remaining gymnosperms, having lost some parts of archegoniate plants, and acquired some of those of the angiosperms, but not having become true anthophyte plants, and, as is generally the case with intermediate types, being less resistant, less capable of further evolution, and therefore doomed to extinction."

Lotsy also (1911, p. 361), as well as Arber and Parkin, regard Gnetales as a terminal branch of the gymnosperms, from which the angiosperms can in nowise be derived phylogenetically.[1]

We are of the same opinion: the Gnetales gave origin neither to the angiosperms nor to any other group (and from that standpoint we cannot regard the term "intermediate," applied to the Gnetales by Kuznetzov, as an especially appropriate one); they form one of the terminal branches of the gymnosperms, which has acquired by means of phylogenetic acceleration a series of characters belonging to a superior organisation. They are the forerunners of more highly organised forms (in other words,

[1] Lignier is also inclined to refer the Gnetales to angiosperms.

of angiosperms), and as such, as precursors, are possibly doomed to extinction.

Let us say a few words on the manner in which, according to Wettstein, the inflorescence of the gymnosperms of the type of Ephedra may have been transformed into the flower of angiosperms.

Wettstein (1911) reasons thus. The flowers in all gymnosperms are diclinous, in most angiosperms monoclinous. Had the male flower of the Monochlamydeae, *i.e.* of the most primitive angiosperms, been derived from the single flower of the gymnosperms, it would be difficult, from the morphological point of view, to account for the appearance in the former of the female flower. Now, Wettstein supposes that the monoclinous flower arose from a male inflorescence, in the centre of which appeared a female flower. Such a supposition is inferred by him from the fact that in certain Monochlamydeae (in the Urticaceae, Euphorbiaceae, etc.) occur inflorescences consisting of very much simplified flowers, with female flowers in their centre; not infrequently among the normal diclinous flowers in the Monochlamydeae monoclinous flowers are to be met with. "What now arises accidentally may have also occurred in primeval times and been the starting-point of a form that has subsequently become typical." The origin of monoclinism is connected with the transition from fertilisation by wind to that by insects: but the visits of the latter are useful to the plant only when the insect comes into contact both with the stamens and the stigma; therefore, "through selection, cases of the union of the male and the female organs must have multiplied, and such a circumstance would give rise to the formation of the monoclinous flower."

Thus, according to this hypothesis, the transformation of a diclinous into a monoclinous flower was due to chance. But we have noted above that Welwitschia, differing in that respect from all other gymnosperms, possesses a rudimentary female flower. This rudimentary monoclinous flower is an aboriginal phenomenon, and not an effect of reversion. Welwitschia shows us how a diclinous flower may be transformed into a monoclinous one: not by means of an accidental occurrence of a female flower in a male inflorescence, but by the female organ appearing spontaneously in a male flower. In addition to which the

process is not accidental, but determined by law: in the male flower the female organ *must* appear; in Welwitschia is shown for the first time what will become the rule in the higher angiosperms.

Kuznetzov (1914, p. 387) seeks for the ancestral types of angiosperms not among the higher gymnosperms, but among the lower, such, for instance, as the Cordaitales.

Thus both the Bennettitales and the Gnetales strive independently of one another to embody the type of the angiosperm flower. At the same time, neither are the ancestors of the angiosperms, and the suggestions of superior organisation have been acquired by means of phylogenetic acceleration.

3. The CASUARINACEAE are shrubs and trees, distributed chiefly in Australia and the Malay Archipelago. They all belong to the genus Casuarina, the only one in this very singular family. In outward form they resemble an arborescent horse-tail or an Ephedra; as in the horse-tail, their leaves are reduced in size, and the branches are brittle at the nodes. As the Casuarinaceae have seeds encased in a fruit and are dicotyledonous, they are included among the dicotyledons and are placed lowest in the scale, next to the willows and birches, being grouped in a separate order, the Verticillatae (Engler, Wettstein, Karsten, Coulter).[1]

The Casuarinaceae are distinguished by their very primitive organisation: the flower is very simply constructed, the type of the structure of the stomata recalls the Conifera; moreover, chalazogamy occurs, *i.e.* during the process of the fertilisation of the ovule, the pollen-tube penetrates through the chalaza, not the micropyle. To the primitive characters of the Casuarinaceae may be further referred the presence in the ovules of not one, but many, sometimes even twenty, embryo-sacs, whereas not only in all the remaining angiosperms, but in the gymnosperms as well, only one embryo-sac, or megaspore,

[1] Hallier (1908), however, places them in the proximity of the Quercineae, regarding them as degraded Terebinthaceae. We may also note the original view of Greguss (1918), according to which the Casuarinaceae constitute a separate group of angiosperms, distinct both from monocotyledons and dicotyledons; in his opinion they are derived from Palaeozoic Sphenophyllaceae through the horse-tails and Ephedra. Whatever be their origin, it seems to me that much may be said in favour of their separation into a distinct group.

develops in the ovule (megasporangium); even in many heterosporous fern-like plants only one megaspore develops in the megasporangium.

But along with these primitive characters, the Casuarinaceae show characters of a superior organisation: both the male and female flowers are clustered together in inflorescences, the posterior locule of the ovary atrophies, of the 2-4 ovules originally developing only one attains maturity, fertilisation is duplex, the integument of the seed unites with the perianth, the seed is exalbuminous, two cotyledons are present, and there are vessels in the fibro-vascular bundles. Such characters do not harmonise with the generalised, very primitive external aspect of the Casuarinaceae, and this tends to show that in their evolution these plants pushed on in advance of their time.

4. *The lowest representatives of the* MONOCHLAMYDEAE, the most lowly organised group of the angiosperms, display several primitive characters, such as a simple perianth, anemophily, an indefinite number of stamens and parts of the perianth, primitive features in the structure of the embryo-sac, endotropic growth of the pollen-tube, etc. But features of a comparatively high organisation may likewise be found, such as fruit in the shape of a nutlet, syncarpous (carpels united together in one ovary or one pistil) gynoecium, one ovule for the most part and complex inflorescence.

In the majority of Salicaceae the perianth is either absent or rudimentary, and the flowers are dioecious. However, both in willows and poplars individual trees bearing staminate and pistillate amenta, and also amenta with staminate and pistillate flowers mixed together, occasionally occur.[1] Haynes (1906) describes an Indian poplar (*Populus glauca* Haynes, from Darjeeling) with bisexual flowers and a large perianth; some trees were entirely bisexual, some entirely female, some with both bisexual and female flowers (there was not a single male tree). Bisexual flowers are known also in other poplars and in *Salix caprea*. In many other Monochlamydeae may be generally observed a tendency towards a higher, bisexual type: in the male flowers may often be found the rudiment of a pistil, and in the female flowers that of the stamens.

[1] Sargant, "Silva Americana," ix, p. 151; Pax, 1894, pp. 31-32, 33.

5. With reference to the POLYCARPICAE (Ranunculaceae, etc.) Kuznetzov (1914, p. 396) says, "By their brilliantly coloured perianth, very early separated into a calyx and a corolla, they overtook both themselves and the Monochlamydeae in their course of evolution, remaining in other peculiarities of structure at a very low stage of development." As primitive characters we may note a large and indefinite number of stamens, pistils and parts of the perianth; a spiral, acyclic disposition of the floral organs; apocarpy (each carpel forming a separate pistil), etc. But it is not only in the flower that the Polycarpieae display primitive characters. Thus in some of the Magnoliaceae the xylem exhibits a structure which is characteristic of gymnosperms: vessels are wanting, and the tracheids have bordered pits.

6. With regard to some CARBONIFEROUS GYMNOSPERMOUS SEEDS Seward (1917, pp. 303-304) says, "Among the numerous types of Palaeozoic seeds are several which invite comparison with the fruits or carpels, apart from the seeds, of angiosperms. Impressions of Samaropsis seeds bear a close resemblance to the laterally expanded fruits of the common crucifer *Thlaspi arvense*; the ribbed testa of Hexagonocarpus and other genera recalls the fruit-wall of Alstroemeria; the recently described Lower Carboniferous seed *Thysanotesta sagittula* Nath. simulates a carpel of Erodium. These and similar instances of a close parallelism in external features between organs that are not homologous, though in themselves of no morphological significance, are at least interesting as illustrating the plasticity displayed by reproductive structures, which in the Palaeozoic period marked a morphological achievement comparable in its importance with the still greater achievement represented by the highly specialised fruits of the modern flowering plants. *The range in form and surface-features of angiospermous fruits was foreshadowed by Palaeozoic seeds.*[1] Structural types, and in some cases, superadded to these, features which may reasonably be supposed to have facilitated dispersal, had been acquired by the seeds of Palaeozoic plants in forms that in a much later period were adopted by fruits even to a greater degree than by seeds. Characters useful in seed-dispersal,

[1] Italics are mine.

that are now shared by fruits and seeds, are illustrated by the fleshy and possibly edible seeds of extinct gymnosperms, the plumes and hairy beak of Gnetopsis and Thysanotesta suggestive of feathery stigmas and other appendages. The lacunar sarcotesta of Aetheotesta, the thick endotesta of Pachytesta, and the air-chamber of Codonospermum, are strictly comparable with aids to buoyancy in fruits of existing flowering plants. The *mucilage-hairs and superficial cells in Physostoma and* Stephanospermum may be compared with the thick mucilaginous investment of the megaspores of recent water-ferns and with similar tissues of some angiospermous seeds."

7. Contemporary trees are characterised by the faculty of depositing an infinite quantity of phloem outside the *cambium, and of xylem within.* And *it is worthy of note* that in the Palaeozoic times all the vascular plants possessed that capacity. Lepidodendrons and sigillarians, which are now regarded as club-mosses, were formerly grouped with the gymnosperms on account of that very feature. Of all the contemporary Pteridophyta Isoëtes, a distant relation of the gigantic fossil arborescent club-mosses, and perhaps a few others, alone have preserved puny remnants of a capacity for secondary growth.

Some recent conifers have in the medullary rays vessels conducting water. These vessels, penetrating the xylem between pith and bast, serve as a water connection between the outer and the inner layers of wood. But an *exactly similar contrivance is to be found in the wood of* the arborescent Palaeozoic club-moss Lepidodendron. The two parallel structures must have evolved quite independently, says D. Scott (1911).

Consequently, the Palaeozoic lepidodendrons, undoubted club-mosses, in two important characters approach the higher seed-plants: in the capacity for secondary growth and, as we shall show presently, in the tendency to produce seeds.

8. The higher plants, gymnosperms and angiosperms, have spores of two kinds, male, or microspores, and female, or megaspores. In the PTERIDOPHYTA the spores are normally of one kind, but in various classes of these

plants (Lycopodiinae, Filicinae, Equisetinae), quite independently, the formation of two kinds of spores may be observed, namely (1) in the heterosporous club-mosses, lepidodendrons, sigillarians, Isoetaceae, Selaginellaceae; (2) in the heterosporous ferns of the Marsiliaceae and Salviniaceae (in both families quite independently of one another); and (3) in the horse-tails of the Calamariales group (Calamites). In all the lower groups named, the possession of heterospores is a precession of the condition that we shall subsequently find in the higher.

9. Mosses, as is generally known, represent a terminal branch of development: they have not given rise to pteridophytes. Now, we know them to possess organs that are imitations of corresponding structures in seed-plants—leaves, rhizoids, stems and flowers (thus, in Polytrichum, on the apices of the stems we observe "flowers" consisting of aggregations of antheridia; such "flowers," are surrounded by modified leaves of a yellow or reddish hue). None of these organs, however, is homologous with any of the structures of the higher plants bearing the same name: it would be sufficient to mention that the leaves of the perianth in seed-plants surround the sporangia, not the sexual organs. Nevertheless, says Velenovsky (1905, p. 151), it cannot be denied that the morphological structure of mosses strikingly corresponds to that of seed-plants. He therefore comes to the conclusion that "dieselbe Form kann aus welchen Komponenten immer aufgebaut werden; oder in dem organischen Stoffe des Pflanzenreiches sind latente morphologische Programme enthalten, welche sich auf jedem beliebigen Organe verkörpern können. Diese Verkörperung wird durch die Lebensbedingungen hervorgerufen."

10. In the homoflagellate chlorophycean alga *Coleochaete pulvinata* the fertilised oogonium is enveloped by a covering consisting of vegetative cells, thus forming a kind of *fruit*. As another feature of high structure may be mentioned an oogonium with a pedicle, and colourless spermatozoids (Lotsy, 1907, pp. 191-194).

Development in the same direction is exemplified in a very singular group, the stoneworts or Charophyta: they also possess something in the nature of a fruit (an oogonium

encased in a thick, coriaceous covering). The spermatozoids in the Charophyta are spirally twisted, like those of the ferns, and are supplied with two flagella, as in the club-mosses ; in germination the zygote produces a filament, on which the adult plant appears in the shape of a bud ; this filament is compared to a prothallus. The oogonium of the Charophyta bears a certain resemblance to an archegonium (Lotsy, 1909, p. 54). Charophyta in general represent a relatively highly organised group. Velenovsky (1905, p. 84) draws attention to the following characters denoting their high organisation : the thallus is differentiated into a central axis with indefinite, and leaves with definite, growth ; the leaves are disposed in regular whorls ; the lateral branches grow from the axils of the leaves ; the reproductive organs are regularly disposed on the leaves ; there are true rhizoids ; the male and female sexual organs are complex and somewhat recall what we observe in mosses ; asexual spores are wauting. Some authors (Cohn) were disposed to refer the Charophyta to the lower mosses ; but at the present time such a view is held to be erroneous. Lotsy (1909, p. 58) maintains that the Charophyta cannot be the ancestors of the Archegoniata, as the oögonium of the Charophyta is not homologous with the archegonium. According to Velenovsky (1905, p. 84) the Charophyta and the mosses cannot be placed in any close relation towards each other : they represent two parallel branches of development, entirely independent of one another. K. I. Meyer, who has given an excellent summary of the opinions held on the origin of mosses, thinks (1916, p. 34) that mosses owe their origin to the Phaeophyta.

Thus, whichever may be regarded as the ancestors of the archegoniates, whether the Chlorophyta (as think Pringsheim, Chelakovsky, Lotsy and others) or the Phaeophyta (Hallier, Potonié, K. Meyer), one thing is clear, that a tendency towards the formation of characters distinctive of a superior organisation is exhibited quite independently by various groups. The Charophyta are one of the lateral branches, which by means of phylogenetic acceleration has reached a considerable height in certain respects, remaining in others at a very low level of structure.

Among the homoflagellate Chlorophyta may be found

species "mimicking" the higher plants. Such, for instance, is the well-known Caulerpa. The separate parts of it are sharply differentiated: we find a "stem," to which "leaves" are attached, colourless thread-like "rootlets" (rhizoids), by which mineral substances are extracted, penetrate the soil. Some species of this genus, such as *Caulerpa hypnoides*, possess bipinnate "leaves." Similarly, Bryopsis, another chlorophyte of the same group, is supplied with very complex "leaves" and colourless rhizoids, which penetrate the soil and perform the functions of a root.

We may, finally, take one more example. In the phaeophyte Laminaria is observed a secondary growth as if by means of a cambium. This feature was still more pronounced in the Palaeozoic alga Nematophycus (Scott).

2. UNICELLULAR ANIMALS

In the Protozoa we meet with several structures which will subsequently appear in the Metazoa in the shape of perfect and complex organs.

The *Foraminifera* have shells very much resembling those of the gastropod and cephalopod Mollusca. It was owing to this feature that former investigators, notably Lamarck, referred these Protozoa to the Mollusca. The polythalamous (many-chambered) Foraminifera are very much like the Nautilidae; even the method of the accretion of new chambers is the same. The Foraminifera *Orbitoides stella* and *O. stellata*, from the Nummulitic limestone (Eocene) of Bavaria, very much recall a starfish (Fig. 2). Some Protozoa exhibit segmentation of the body. The large gregarine, *Taeniocystis mira* (Fig. 3), over 1 mm. in length, has an elongated, worm-like, metamerically segmented body, and very much resembles a tape-worm. A parasitic flagellate,

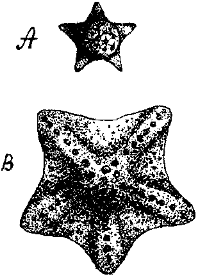

FIG. 2.—Echinoderm-like Foraminifera from the Eocene Nummulite Limestone of Bavaria. *A*, *Orbitoides stella*; *B*, *Orbitoides stellata*.
(From O. Abel, "Lehrbuch der Paläozoologie." Jena, 1920, G. Fischer.)

Cyclonympha strobila, inhabiting the intestine of Japanese termites, is likewise segmented and looks very like a Taenia; its length is 0·11-0·17 mm. (Dogiel, 1917).

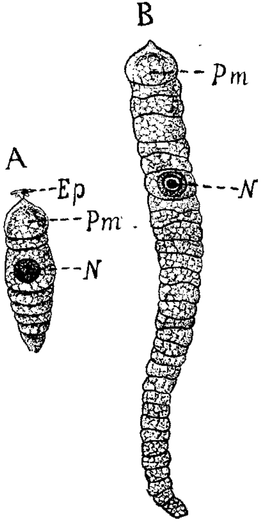

FIG. 3.—*Taeniocystis mira*, a segmented gregarine. *A*, young individual; *B*, nearly full-grown.
Ep, epimerite; *N*, nucleus; *Pm*, protomerite.
(From F. Doflein, "Lehrbuch der Protozoenkunde." 4 Aufl. Jena, 1916, G. Fischer.)

A Mediterranean pelagic flagellate, *Leptodiscus medusoides*, of the Cystoflagellata, measuring 1-1½ mm., very much resembles the young of certain medusae. These protozoa swim like a medusa, contracting their discs, on the lower surface of which, as in the medusa, muscular fibres may be observed. Another cystoflagellate, *Craspedotella pileolus*, from California, bears a still stronger

likeness to a medusa in possessing a structure recalling a velum on the lower margin of its "umbrella."

The Protozoa not infrequently have contractile fibres, or *myonemes,* sometimes supplied with a rudimentary transverse striation and imitating, as it were, the transversely striated muscles of the Metazoa. A ciliated infusorian, Umbellaria, possesses spirally folded, stinging filaments, recalling the nematocysts of certain Coelenterata and of other groups. Quite independently of the ciliated infusoria similar organs are developed in other types of the Protozoa, as in some Dinoflagellata (for example, in Polykrikos).

Certain Infusoria are observed to possess structures resembling nerve fibres (*neurophanes*). R. Sharp (1914) has lately discovered a very complicated neuromotor *apparatus, apparently possessing nervous functions,* in a ciliate infusorian, Diplodinium, from the stomach of cattle (Fig. 4). It consists of a central mass lying in the ectoplasm on the dorsal side, and gives forth a number of branches. One of these branches leads to a ring surrounding the oesophagus or pharynx, others to bunches of cilia serving as motor organs. Fibres connect the circumpharyngeal nervous ring with the walls of the oesophagus. The similarities with the nervous system of multicellular organisms are obvious; such are the dorsal position of the nervous ganglion situated above the oesophagus, the presence of a circumpharyngeal nervous ring (as in worms, molluscs, arthropods) connected with the nervous ganglion. A similar "neuromotor" centre was found by Yocom (1918) in the ciliate infusorian Euplotes. At the time of division the new neuromotor apparatus is formed independently of the old one, by an insinking of the outer surface of the pellicle. Dogiel draws attention to the fact that the neuromotor apparatus in Euplotes is formed from the ectoplasm, just as the nervous system of Metazoa is produced from the ectoderm. In both cases the nervous apparatus becomes pushed inwards or invaginated from the surface. Rees (1921) has described a similar neuromotor centre in *Paramecium caudatum*; micro-dissection experiments showed that the coordination of movement of the cytopharyngeal membranelles is interrupted when the neuromotor fibres are cut; extensive destruction of structures in the region of

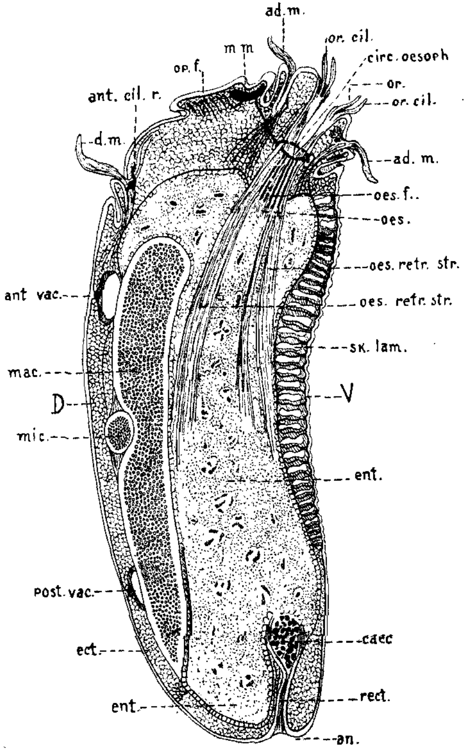

FIG. 4.—*Diplodinium ecaudatum* (forma typica), a parasitic infusorian. Median sagittal section.

ad. m. adoral membranelles; *an.* anus; *ant. cil. r.* anterior ciliary roots; *ant. vac.* anterior contractile vacuole; *circ. oesoph. ring*, circumoesophageal ring; *caec.* caecum; *D.* dorsal side of body; *d.m.* dorsal membranelles; *ect.* ectoplasm; *ent.* endoplasm; *mac.* macronucleus; *mic.* micronucleus; *m.m.* motor mass (motorium); *oes.* oesophagus or cytopharynx strands; *op. f.* opercular fibres; *or.* oral opening, mouth; *or. cil.* oral cilia; *post. vac.* posterior contractile vacuole; *rect.* rectum; *sk. lam.* skeletal laminae; *V.* ventral side of body.

(From R. Sharp, in Univ. California Publications. Zoology, xiii. N. 4, 1914. University of California, San Francisco, U.S.A.)

the neuromotor centre or motorium destroyed coordinated movement of the peripheral cilia. Complex structures, also apparently bearing relation to nervous functions, occur in the Flagellata (see a review on the subject by Yocom). The structure of the Protozoa thus actually appears to be extremely complex.

Most infusoria are provided with a rudimentary digestive apparatus in the shape of a mouth, pharynx and a kind of anus.

In *Cyclopostium bipalmatum*, a parasitic infusorian from the intestine of the horse, according to Dogiel's (1923) observations, during copulation, the male pronucleus is transformed into a *spermatozoon* possessing a well-marked head with a kind of perforatorium at its anterior end and a long tail. The spermatozoon coalesces with the female pronucleus of the partner infusorian. We have therefore in Cyclopostium, says Dogiel, a most peculiar case of a protozoon producing in its body a typical spermatozoon, which is expelled into the surrounding medium and finds its way to the female nucleus of the conjugant through the mouth and pharynx of the latter, just in the same way as do, for instance, the spermatozoa of Anthozoa. "The facts newly discovered make the conjugation of Infusoria resemble very closely the process of fertilisation in multicellular organisms."

3. ANIMALS (METAZOA)

1. In the structure of adult Tunicata we find characters belonging to vertebrates: the gill-slits pierce the walls of the anterior part of the alimentary canal, the pharynx is supplied with a ciliated glandular fold, the so-called endostyle, a homologue of which is possessed by Amphioxus, by the larvae of lampreys (Ammocoetes), and by the embryos of all vertebrates. (In adult vertebrates a corresponding outgrowth of the ventral wall of the branchial part of the alimentary canal is transformed into the thyroid gland.) Beneath the brain of the Tunicata lies a gland, which communicates with the anterior part of the pharynx: it is compared with the pituitary body of the vertebrate brain.

Digestion in tunicates is of a vertebrate character. Kravkov (1889, p. 70) found that the digestive secretion

extracted by him from Cynthia operates upon proteins in an acid medium: Cynthia, like vertebrates, thus possesses a *peptic digestion*, whereas the digestive ferment of invertebrates is trypsin.

2. As another manifestation of phylogenetic acceleration we regard the occurrence of vertebrate features in the ENTEROPNEUSTA (Balanoglossus and others) and in the PTEROBRANCHIA (Cephalodiscus, Rhabdopleura), namely, rudimentary segmentation (into three segments), the presence of gill-slits (or branchial grooves in *Rhabdopleura*) in the anterior part of the alimentary tract, and a rudimentary notochord.

3. The CEPHALOPODA, notably the Dibranchiata, exhibit a tendency to surround the central nervous system with an internal cartilaginous skeleton, similar to what occurs in vertebrates. Thus in Sepia the cephalic nervous ganglia, the eyes, and the organs of "hearing" (statocysts) are surrounded with cartilage, and the animal possesses nuchal and fin cartilages, etc. In structure the cartilage somewhat resembles that of vertebrates.

4. The SELACHII anticipate some characters belonging to more highly organised vertebrates, including mammals. Thus, in these fishes may be observed a predisposition to establish a communication between the nasal and buccal cavities (as in the Cestraciontidae and the Holocephala), which is the first step towards pulmonary respiration; they possess dorsal ribs, a well-developed cerebellum (whereas in the Amphibia and in most reptiles the cerebellum is rudimentary); they exhibit a tendency towards the transformation of the kidneys into a metanephros, and the presence of very perfect copulatory organs (pterygopodia);[1] in some sharks (Pristiurus) in the earlier stages of their development may be observed the rudiments of an amnion. In many of them, finally, there is a disposition towards the formation of a placenta, which, among mammals, is first fully developed not earlier than in some

[1] Reproduction by means of copulation, being also connected with viviparity, is an indubitable feature of a higher organisation than is the direct deposition of eggs and sperms in the water, as occurs in the majority of Teleostomi. Still, copulation and viviparity, as well as in the Selachii, are observed in several Teleostei, *e.g.* the "viviparous blenny," *Zoarces viviparus*, of the Blennidae, in the Baikal Comephorus, in the Embiotocidae, inhabiting the Pacific, and in some of the Cyprinodontidae.

Marsupialia (see below). In the dogfish *Mustelus laevis* Risso, as was already known to Aristotle, the walls of the uterus (*i.e.* the posterior portion of the oviducts) form vascular outgrowths which enter into the folds of the yolk-sac wall; each embryo is supplied with its own placenta, so that the uterus is partitioned into several chambers: something of the kind is observed in the shark Carcharias. In some (as in the skate Pteroplatea) the inner surface of the uterus is supplied with filaments, by which a milky secretion is introduced into the spiracles of the embryo. This secretion is elaborated in certain *glands embedded in the filaments. For squeezing the* milk from the filaments special superficial muscles are present. Both the filaments and the walls of the uterus are supplied with a large number of vessels (Alcock, 1902).

5. In the HOLOCEPHALA (Chimaera, etc.) the skull is autostylic, *i.e.* the palatoquadrate, as in the Tetrapoda, is fused with the skull. In these fishes the nares are connected with the buccal cavity.

At the same time, it is now established that the Selachii *(including the Holocephala) did not give rise to the higher* fishes (Teleostomi), but constitute a branch parallel to these.

6. The Selachii and Holocephala are characterised by the absence of true (cartilage) bones; scales, if present, have the form of dermal teeth, the jaws consist of Meckel's cartilage and the palatoquadrate alone. But in the extinct Palaeozoic ACANTHODII, which are usually grouped with the sharks, we meet with very peculiar scales, somewhat recalling those of ganoids (notably the scales of the Devonian ganoid fish Chirolepis); upper and lower jaws enclosed in a dense "bone-like" tissue, as in higher fishes (Teleostomi), with teeth sometimes inserted in these "bones" (in the Lower Devonian Ischnacanthus).

Finally, a most remarkable resemblance to the Teleostomi is exhibited in the pectoral girdle: in Diplacanthidae we find dermal "bones" in the shape of clavicular and supra-clavicular plates. In the region of the pectoral girdle Acanthodes had a dermal "ossification" which is compared to the cleithrum. And yet the absence of a dermal skeleton constitutes a characteristic feature of the Selachii, in distinction to the higher fishes or Teleo-

stomi. Huxley regarded the Acanthodii as transitional forms between the Selachii and Ganoidei; Smith Woodward places them among the Selachii, which they approach in the absence of gill-covers and in the structure of the skeleton;[1] Jaeckel (1911) allies them to the Teleostomi. We consider the Acanthodii as constituting a separate class, the distinguishing features of which are the peculiar structure of the mandibular and branchial apparatus, the pectoral girdle and the scales, as well as the absence of true osseous tissue. The Acanthodii are not the ancestors of the Teleostomi. Like the Bennettitales, they form a lateral branch, combining the characters of the Selachii and Teleostomi.

7. *In the North-American fresh-water fishes of the* family PERCOPSIDAE, which is now referred to the order of Salmopercae, along with very lowly structural features we encounter very high ones. In outward form Percopsis is intermediate between a trout and a ruff (pope): like the Salmonidae, which belong to the lowest Teleostei, it has an adipose fin behind the dorsal; but, on the other hand, like the Percidae, which are referred to the highest Teleostei, it has strong spines in the dorsal and anal fins. The ventral (pelvic) fins, as in the Acanthopterygii, are situated below the pectoral, but their skeletons are unconnected. The scales, as in the Percidae, are ctenoid; but the air-bladder, as in the Cyprinidae, the Salmonidae, the Clupeidae and other lowly organised fishes, communicates with the alimentary tract. The ventral fins are spineless and contain many branched rays, as in lower Teleostei.

8. Some fishes, for instance the Sciaenidae (Pogonias, Corvina, and others), possess an AIR-BLADDER which gives out numerous branching diverticula, the purpose of which is *not known*. In such lizards as geckos, iguanas, Varanus, and especially in the chameleons, the lungs are supplied with long sacs divided into few cells or even possessing perfectly smooth walls. The chameleon makes use of these sacs (in combination with tracheal and pharyngeal ones) when inflating its body on being excited. A remarkable development has been attained by the air-

[1] Although the higher fishes (Teleostomi) occur contemporaneously with the lower Selachii in the Devonian period, there can be no doubt that the Selachii originated long before the Palaeozoic era.

sacs in birds, which is connected with the pneumaticity of their bones: in birds the bones, being usually devoid of marrow, are hollow; through special openings these cavities are penetrated by the diverticula of the air-sacs. Such a peculiarity is directly connected with the power of flight,[1] although in some birds, which fly well, such as gulls and terns, the bones are pneumatic to a small degree only. But the following is very remarkable. Some fossil reptiles (Dinosauria) devoid of the power of flight, nevertheless possessed pneumatic bones. "Thus," says Schimkewitsch, "although there is a certain relation between flight and the pneumaticity of bones, which naturally proceeds from the greater lightness of a pneumatic bone as compared to a solid one, yet pneumaticity itself arose earlier than the ancestors of birds acquired the capacity for flight" ("Lehrbuch der Vergleichenden Anatomie der Wirbeltiere").

Thus even in fishes and reptiles peculiar structures are indicated which will in time develop into organs possessing a relation to flight. As long ago as in 1881 Eisig described peculiar dilatations of the intestinal tract in certain annelid worms (Hesione, Syllis), which he called organs "similar to the air bladder." In these worms, from the anterior part of the tract diverge, one on each side, two large extensible sacs. Both Hesione and Syllis are destitute of gills, and breathe by means of the digestive tube. The sacs just mentioned serve for storing oxygen, which, as Eisig believes (p. 286), may in case of necessity be restored to the intestine. But these organs also play the part of a hydrostatic apparatus assisting the worm to rise and sink in the water, in which case the sacs are either emptied of gas or filled with it (these worms sometimes swim on the surface). However, in Eisig's opinion (p. 289), this function of the sac "does not constitute the only purpose of that organ, nor did it serve as a basis for the formation of the latter"; it is, in fact, quite subsidiary. Thus the "air-bladders" of the annelids present an analogy to the air-bladders of fishes, which, however, are chiefly used as hydrostatic organs. So even in annelid worms organs are

[1] It is only through the possession of air-sacs that a bird is enabled to breathe during flight. These organs accomplish other functions besides: they protect the body from loss of heat, give elasticity to the thorax, and assist in swimming and diving (see F. E. Schulze, 1912, pp. 480-481).

indicated which will subsequently be transformed into lungs.[1]

9. The BRAIN OF FISHES is generally of a more complex character than that of amphibians, its histological structure is more complicated, the number of cells is greater, and the latter possess more numerous processes. Psychically, fishes are probably superior to amphibians, although in other respects they are organised on a lower scale.

10. In 1904 Broili described a remarkable vertebrate SEYMOURIA from the Permo-Carboniferous deposits of Texas, which he at first took to be a stegocephalan, but subsequently described as a primitive reptile of the group of Cotylosauria (see Broili, 1904, p. 580, Figs. 1, 2). The points of resemblance to amphibians are truly remarkable. Williston, however, was disposed to consider this resemblance as a mark of "convergence." But this convergence affects nearly all the features of the structure of the skeleton—the skull, the pectoral and pelvic girdles and the extremities. The only character which caused Watson (1918, p. 293) to refer Seymouria to the reptiles, is the structure of the vertebra: the articular facets of the zygopophyses are horizontal, and the dorsal arches wide and swollen. But, at the same time, the vertebral column is characterised by very primitive features, such as the presence of but *one* sacral vertebra. All of which testifies to Seymouria being a very primitive tetrapod which had acquired some reptilian characters as a result of phylogenetic acceleration.

11. Bolck studied the variations in the lower jaw of adult and young GIBBONS, *Siamang syndactylus*, from Sumatra. The great individual variability of the region of the chin and of the adjoining parts of the alveolar region is very remarkable. Such extreme variability is not met with in any of the remaining monkeys, especially in any of the anthropoid apes. At the same time, this variability in the lower jaw of the gibbon has a marked tendency to develop in the direction reached in the group of Hominidae by the formation of the projecting chin.

[1] We may also note here that the mouth-parts of the Ephemeridae are atrophied and their alimentary tract is incapable of acting as an organ of digestion. Yet it is well developed, and is employed as a balloon during the peculiar dancing flight of these insects.

4. MAN

Neanderthal man, *Homo neandertalensis*, exhibits certain points of structure which in their development have advanced beyond those of contemporary man (*Homo sapiens*). As is known, *H. neandertalensis* or *primigenius* existed in the Old Stone Age, or, to be more exact, in the lower Palaeolithic : he survived only until the end of the Mousterian epoch, since when the remains of *Homo sapiens* (namely, the Cro Magnon race) with all his characteristic features begin to appear. (We may here point out that according to the latest views there are no proofs in favour of *H. neandertalensis* being the ancestor of contemporary man (Keith, 1916, p. 148) ; the same opinion is expressed by Osborn in his book, "Men of the Old Stone Age" (New York, 1921, p. 489)).

Adlof (1907), by means of the Röntgen rays, investigated the teeth of the lower jaw of *Homo neandertalensis* from Krapina, and has compared them with teeth from Taubach which belonged to an individual closely related to the Neanderthal race, as also with the teeth of the *chimpanzee*. *It appeared that the molar teeth in Neanderthal man had advanced in their development beyond those of the chimpanzee and of contemporary man :* the pulp cavity of the tooth in *H. neandertalensis* is considerably larger than that of the chimpanzee and of *H. sapiens*, having increased at the expense of the roots ; the cavity in the lower molars of *H. neandertalensis* sinks below the upper (alveolar) margin of the jaw, while in contemporary man and in the anthropoid apes it lies above that margin (Keith, pp. 147-8, Fig. 50 ; p. 476, Figs. 174-5) ; the crown of the teeth in *H. neandertalensis* is very wide and low, the roots being considerably shorter. The same features characterise the teeth of the Heidelberg jaw ("*H. heidelbergensis*"), which belongs to the same species, *H. neandertalensis* (p. 237). In the character of the teeth, says Keith (p. 148), Neanderthal man has advanced very much beyond the primitive or simian type, while contemporary man has retained the ancient, simian features in his molar teeth. Judging from the Heidelberg jaw, the canines in *H. neandertalensis* have advanced further from the simian teeth than have the canines of contemporary man : they

differ less from the other teeth than do those of contemporary man (*l.c.*, p. 237).

Neanderthal man, while in general possessing a more primitive structure than contemporary man, has other characters of a higher organisation besides those of his teeth. In the chimpanzee a groove betweeu the sides of the nose and mouth may be observed on either side of the skull: it may be found in many primitive races of *H. sapiens*, being absent in the higher; it is absent, or nearly so, in *H. neandertalensis*, who in this respect approaches the higher races (Keith, p. 144). The palate in the chimpanzee is narrow and long; it is the same in Eoanthropus; in contemporary man it is wider, acquiring a horse-shoe shape, but in Neanderthal man it is still wider, especially when compared with the Tasmanian.[1] The width of the palate in percentage of its length is 80% in the chimpanzee, 107% in the Tasmanian, and131% in Neanderthal man (the Gibraltar skull).

The brain of Neanderthal man not only yields nothing in volume to that of the European, but actually surpasses it, to judge from the La Chapelle skull, the capacity of which was 1625 c.cm.

Werth (1921, pp. 169-170, 304) even regards the torus supraorbitalis as a progressive feature in Neanderthal man: it is absent in primitive Lower Tertiary Simiae as well as in recent lemurs; in monkeys and apes the torus occipitalis is well developed only in such specialised forms as the baboons, macaques, the gorilla and chimpanzee, in which it is more pronounced than in Neanderthal man. Moreover, the ramus ascendens of the lower jaw is cast in a more progressive mould than in fossil *Homo sapiens* (namely, *H. sapiens aurignacensis*), and in certain respects is more progressive than in contemporary man: it is higher in Neanderthal man than in *H. aurignacensis*, and its angulus is less primitive than in the latter and in *H. sapiens* (Werth, pp. 185, 313-4). The author referred to agrees therefore with Keith in considering, like Klaatsch (1910, 1912), that *H. sapiens* cannot be derived from *H. neandertalensis*.

Wallace has remarked somewhere that primitive man has obtained from Nature a much more perfect brain than

[1] *l.c.*, pp. 150-151, Fig. 52; cf. also Fig. 110 on p. 328.

was required for his self-preservation. With respect to *H. neandertalensis* this observation is perfectly just. Neanderthal man became extinct, leaving no descendants, and his brain is a feature "prophetic" of the height which will be attained by *H. sapiens*: it is an example of phylogenetic acceleration.

Homo neandertalensis and *Homo sapiens* are two parallel forms which have developed independently of one another. As is assumed by Keith (1916, p. 501), towards the beginning of the Pleistocene period three parallel branches of the human stock already existed—(1) Neanderthal man, (2) *Homo* (or *Eoanthropus*) *dawsoni* (recently discovered in Sussex, England) and (3) *Homo sapiens*.[1]

All the foregoing examples, and they could easily be multiplied, for the entire field of comparative anatomy and morphology is full of them (in chapter iv further illustration of the subject will be given), indicate that :—

(1) New characters arise not accidentally, but in accordance with law, for the regular manifestation in higher forms of features of advanced specialisation, which are, or were at some time, met with in lower forms, cannot be due to chance.

(2) With the development of such characters the struggle for existence and natural selection had obviously nothing to do.

(3) In all the above-mentioned cases evolution proceeds in accordance with law, or, in other words, in a determined direction.

The phenomenon of phylogenetic acceleration, so common in plants as well as in animals, compels us to be extremely careful in the establishment of phylogenetic schemes. Thus, the segmentation of the coelom of the larva of the Echinodermata does not testify to the origin of Echinodermata

[1] Osborn (1921) considerably reduces the antiquity of *H. dawsoni*. In his opinion, Heidelberg man lived in the second inter-glacial epoch (Mindel-Riss), *H. dawsoni* in the third (Riss-Würm; pre-Chellean time), about 125,000 years ago; lastly, Neanderthal man lived between the third and the end of the fourth inter-glacial epoch (75-25,00 years ago). But this in no way modifies the arguments submitted above.

from metameric ancestors, but possibly indicates a definite course of development—in the direction of metameric organisms.

Finally, to avoid any misunderstanding, I think it necessary to point out that the expression "precession of phylogeny by ontogeny" should be regarded as a metaphor. In effect, there is no mysterious precession of the future, nor any incomprehensible repetition of phylogeny by ontogeny. One thing is certain, and that is, development proceeds according to law, or by *Nomogenesis*. As development, both individual and phylogenetic, is governed by law, and as the evolution of characters does not proceed at a uniform rate, then, as a consequence, the process in question gives the impression either of a precession, or a repetition of phylogeny (see also chapter iii, § 4).

It may be thought that the same idea (of phylogenetic *acceleration*) *entered into the vague speculations* of Cope (1868; 1887, pp. 76 *seq.*, 122) on retardation and acceleration in development. K. C. Schneider in his "Einführung in die Deszendenztheorie" (1911, p. 53) even goes so far as to say that "ontogeny may be the forerunner of phylogeny" ("die Ontogenie kann Vorläufer der Phylogenese sein").[1]

SUPPLEMENT

J. A. Philiptschenko has drawn my attention to the following passage in Baer's "Entwickelungsgeschichte der Thiere" (1828, Schol. v. § 2, p. 205-206). In disputing the view that "the embryos of higher animals pass through the forms of the lower" (pp. 199 *seq.*) (*i.e.* in the current expression, "ontogeny repeats phylogeny"), Baer says, "If that were the case, structures which are permanent only in more advanced forms would not be exhibited in a transient condition in the embryos of lower forms. In all mammals in the first stage of development the jaws are as short as in man. The brain of birds during the first third of its embryonic condition much more nearly

[1] I became acquainted with this work after the Russian edition of "Nomogenesis" had been published.

approaches that of mammals than in the adult state. The corpora quadrigemina are not removed to the sides, the *olfactory lobes are hollow and thick; there is even* something in the shape of a fornix. In the birds' tarsus one bone is formed from several cartilages. In the chicken the eyes are much closer together, whereby a resemblance to a human face is acquired. Young lizards possess a very large brain. The tadpole is provided with a true beak, like a bird's. The embryo of the frog, in the first stages, is tailless, a condition observed only in the highest mammals, for even the adult frog possesses an inner tail, by which term the long caudal vertebra may be called. Centipedes, mites and hydrachnids, when hatched, possess three pairs of legs, like insects with metamorphosis into the adult stage."

CHAPTER III

EVOLUTION FOLLOWS A DEFINITE DIRECTION OR IS DETERMINED BY LAW

> Frustra fit per plura, quod fieri potest per pauciora.
> NEWTON, "Philosophiae Naturalis Principia Mathematica," iii.

> Any newly defined relation, new law or rule in the variation of organisms, in the course of heredity or the phenomena of hybridisation and reproduction, which we may discover, *cancels* the theory of Darwin. For the Darwinian process requires as a necessary condition a complete indefiniteness in all these processes, a veritable chaos, from which order must emerge of itself, under the effect of one determined principle, that of utility, or preservation from destruction. N. STRAKHOV, 1889, pp. 202-203.

> As in the domain of inorganic nature, so in the domain of organic nature *fortuity is wanting*, and the fit originates in many hard parts of the body through laws which are in the main similar to growth—laws the modes of which we see and measure, the causes of which we do not and may never understand, but nevertheless laws and not fortuities or chance happenings.
> H. F. OSBORN, 1909, p. 225.

DARWIN believed that characters vary in all directions, like, let us say, rays issuing from the sun. "Our theory," as we read in the "Origin of Species," "includes no fixed law of development, causing all the inhabitants of an area to change abruptly, or simultaneously, or to an equal degree" (chap. xi, p. 291).

We, on the contrary, claim that variation of characters is confined within certain limits, that it follows a definite course, like an electric current moving along a wire.

According to the first assumption, that of Darwin, the formation of characters may be due to chance; according to the second, chance is excluded as an agency in variation.

The facts presented in the previous chapter clearly show that cases may occur in which the course of evolution seems to be predetermined. If in the young ammonites characters arise that will subsequently be manifested in more recent deposits in adult individuals of other, phylogenetically younger forms, there can be no question of chance. But in favour of the proposition that evolution is subject to law, that it is nomogenesis, testify (in addition to the phenomena of phylogenetic acceleration (chap. ii)) the following :—

1. *Facts* from palaeontology and comparative anatomy: here we plainly see the course which evolution follows.

2. Cases in which similar characters are developed in two or more series of forms. The phenomena of convergence, parallelism, analogous variations, etc., will be discussed in chapters iv-vi.

3. The process of individual development, or ontogeny.

As a classical case of development in a determined direction, or orthogenesis, may be instanced the evolution of Paludinae from the Pliocene of Slavonia: the smooth *Paludina neumayri* by means of a series of mutations, imperceptibly yet steadily leads to the more recent *P. hoernesi* with a shell of such complex structure that the latter species is now referred to the group Tulotoma.[1] "If we were to mould in clay a model of *P. neumayri*," says Neumayr, "and should wish to transform it into *P. hoernesi* in the simplest way, we could not do it otherwise than as it has been done by Nature: development pursues the most direct course."

In a very instructive paper (1915, reprinted 1917) D'Arcy Thompson shows that by means of some simple mathematical operations it is possible to transform one organic form into another. The differences between forms not far removed in the system are just such as might have been brought about by a slight change in the system of forces, internal and external, to which living organisms are exposed.

[1] Neumayr und Paul, 1875, p. 98; Neumayr, 1889, p. 57.

Let us take a marine fish Scarus. Deforming the coordinates of Fig. 5 into the curved orthogonal system, we at

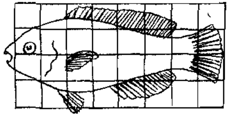

FIG. 5.—SCAURUS.
(From D'Arcy W. Thompson, "On Growth and Form." Cambridge University Press, 1917.)

once obtain a representation (Fig. 6) of a not very far distant genus, Pomacanthus. Fig. 7 represents with Car-

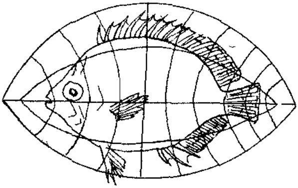

FIG. 6.—POMACANTHUS.
(From D'Arcy W. Thompson, "On Growth and Form." Cambridge University Press, 1917.)

tesian coordinates a common Diodon, or porcupine fish. Its vertical coordinates being deformed into a system of

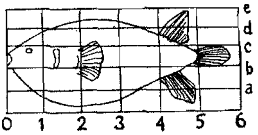

FIG. 7.—DIODON.
(From D'Arcy W. Thompson, "*On Growth and Form.*" Cambridge University Press, 1917.)

concentric circles, and its horizontal coordinates into a system of hyperbola-like curves, the old outline of the

Diodon is transformed into that of an allied although very different looking fish, the sunfish, Mola (or Orthagoriscus, Fig. 8). Figs. 9 and 10 give the outlines of a human skull and that of a chimpanzee.

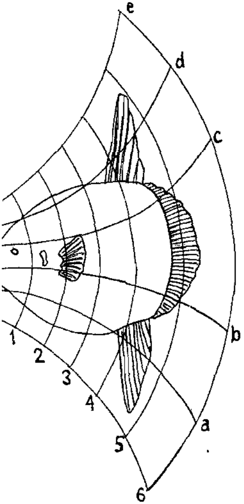

FIG. 8.—MOLA.
From D'Arcy W. Thompson, "On Growth i Form." Cambridge University Press, .7.)

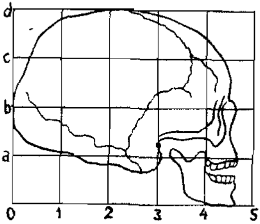

FIG. 9.—SKULL OF MAN.
(From D'Arcy W. Thompson, "On Growth and Form." Cambridge University Press, 1917.)

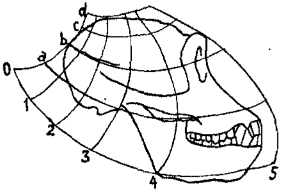

FIG. 10.—SKULL OF CHIMPANZEE.
(From D'Arcy W. Thompson, "On Growth and Form." Cambridge University Press, 1917.)

If we embrace in our vision the evolution of the whole organic world, we perceive that it proceeds in a determined direction. Nature strives, that is to say, to *insure in the best possible manner the preservation and welfare of the developing progeny*, both in plants and in animals. In the higher vertebrates, the viviparous Mammalia, the development of

the embryo in the body of the mother has become the rule. The same phenomenon is sporadically met with in many lowly organised animals, such as in certain Coelenterata, worms, Echinodermata, insects, bony fishes. In seed plants, *i.e.* gymnosperms and angiosperms, the fertilised ovule, while still in the body of the mother plant, passes through its cycle of development leading to the formation of the embryo, in which are already laid down the principal organs —the root with, sometimes, secondary roots, the stem and the leaves.

Evolution follows a definite course, which is shaped both by external (geographical), and internal (autonomic) causes.

In this chapter we shall consider some facts relating to autonomic orthogenesis.

1. AUTONOMIC ORTHOGENESIS

That there are intrinsic and constitutional agencies laid down in the chemical structure of the protoplasm, which compel the organism to vary in a *determined direction*, may be inferred from the fact that not infrequently evolution proceeds, as it were, in face of the environment, in a direction leading the organism to destruction. As an example, may be adduced the gigantic dinosaurs and other giants (whales, Sequoia, etc.), which are all doomed to extinction.

It is perfectly obvious that an organism may pass through a certain cycle of development under the influence of internal causes, independently of any changes in the environment. In support of this view we may refer to the entire process of embryonic development. We may further take as an example the cycle of development of one of the races of the rotifer *Anuraea aculeata*. From unfertilised (parthenogenetic) ova are successively hatched the forms *brevispina*, *valga*, *curvicornis*, in which the general size and the length of the posterior styles gradually lessen ; after a time appear the males, and from the fertilised ovum is produced the large

typical *A. aculeata*. In this example variation due to inner constitutional causes is clearly exhibited. The researches of Woltereck (1911) have shown that it is hardly possible to induce Daphnia to resort to sexual reproduction during the first period of the existence of a brood produced from winter eggs. But after a series of parthenogenetic generations, " the tendency towards the production of males arises with an irresistible force." To the same class of phenomena may be referred sexual dimorphism, as also polymorphism in bees, ants, termites, etc., alternation of generations in medusae, salps, etc.

In the Aphidae, as is generally known, there also occurs an alternation of generations. Clodnicki (1921, p. 90) believes that no external agency can be regarded as exerting a direct influence on the production of the sexual generation or of the winged individuals in aphids. The fact that the life-cycles of various species of aphids existing in identical or nearly identical conditions, follow different courses, testifies to the species being not only morphologically, but biologically distinct (p. 52). The alternation of generations is predetermined by " a particular inner mechanism acting with periodical regularity."

The opinion is rather prevalent that the evolution of organisms may be explained by the influence of external conditions alone : organisms have varied in correspondence with the changes in the inorganic world. Account must be taken of the fact that such an assumption implies the admission of an inherent capacity of the living being to respond in a fit manner to stimuli, as we have fully indicated in chap. i, § 1. But apart from this, the opinion just mentioned is one-sided. Evolution cannot be accounted for by external influences alone. In this connection it would be sufficient to observe that every now and then organisms and groups of organisms arise and become extinct without any perceptible influence on the part of the external world. What physical causes involved the extinction of dinosaurs,

pterodactyls, and Theromorpha during the Mesozoic era? With what vertebrates had the gigantic dinosaurs to contend for existence?

As has been indicated by Neumayr and Paul (1875, pp. 102-103), evolution follows a definite course in ammonites independently of external conditions. Many groups of sea inhabitants, *e.g.* Ammonidea, says Salfeld (1921, p. 56), show that the same transformation (mutation) is produced in stable bionomical environment, as well as when the environment changes.

Waagen has noticed that in certain fossil brachiopods radial striae appear on the shells of the more recent species. Thus, in the Lower Carboniferous *Meekella oliveriana* the shell is smooth, in the Upper Carboniferous *M. striatocostata* and *M. eximia* radially ribbed in a marked degree. The same is observed in the allied genera Streptorhynchus and Derbya. Waagen thinks that this peculiarity in the sculpture of the shell is due to an "inner law," which, at a definite time, everywhere, produces certain characters, quite independently of external conditions.

On the other hand, vast changes in the climate, recurring every now and then, have quite an insignificant influence on the evolution of the organic world. A striking instance of this is afforded by the glacial epoch. It is difficult to conceive a greater change of decoration in the scene of nature than that which accompanied the enveloping of a vast area of the earth in the northern hemisphere in a massive layer of ice. And yet the glacial epoch exerted an insignificant influence on the production of *new* forms. The effect of the catastrophe on the geographical distribution of organisms was, of course, immense; some forms became extinct, others migrated: but very few new forms were brought to life in comparison with the tremendous work of destruction and selection accomplished by Nature. The insignificance of the effects of the struggle for existence is here displayed with uncommon force.

That the effect of external conditions alone cannot account for the great diversity of characters has already been indicated by Darwin ("Variations of Animals and Plants," chap. xxiii): under the same external conditions diverse variations have often been produced, while, on the other hand, the organism quite often persistently preserves its characters under the most diversified conditions.[1] Darwin believes "*that in most cases the conditions of life play a subordinate part in causing any particular modification, like that which a spark plays*, when a mass of combustibles burst into flame—the nature of the flame depending on the combustible matter, and not on the spark" (*op. cit.* chap. xxiii). The organisation or constitution of the being which is acted on, is generally a much more important element than the nature of the changed conditions, in determining the nature of variation (*ibid.*). "Each trifling variation is governed by law, and is determined in a much higher degree by the nature of the organisation, than by the nature of the conditious to which the varying being has been exposed" (*ibid.* chap. xxvi). And further, "Although every variation is either directly or indirectly caused by some *change in the surrounding conditions, we must never* forget that the nature of the organisation which is acted on, *is by far the more important factor in the result.* We see this in different organisms which when placed under similar conditions vary in a different manner, whilst closely allied organisms under dissimilar conditions often vary in nearly the same manner. We see this in the same modification frequently reappearing in the same variety at long intervals of time, and likewise in the several striking cases given of analogous or parallel variations. Although some of these latter cases are due to reversion, others cannot thus be accounted for" (*op. cit.* chap. xxviii).

In a very interesting correspondence between Darwin and Huxley, following on the reception by the latter of a copy of the "Origin of Species," the subject we are engaged in was broached. In a letter dated November 23rd, 1859, Huxley writes, "It is not clear to me why, if continual physical conditions are of so little moment as you suppose, variation should occur at all?" In a letter dated

[1] See also "Origin of Species," chap. i, p. 6.

25th November, written in answer to this, Darwin exclaims, "If, as I must think, external conditions produce little direct effect, what the devil determines each particular variation?"[1]

It sometimes happens that, in spite of varying external influences and the difference of "landscape," the organism produces the same characters in different localities. The following is one of the most striking examples of this. According to the observations of R. E. Regel (1912, p. 473), from one and the same barley, *Hordeum vulgare leiorhynchum nekludovi*, a new form has been obtained in two different localities, by means of regressive mutation. This form, the barley of Stassevitch (*H. vulgare rikotense stassewitschi*), is distinguished by the disappearance of the pigment that gives a black colour to the glume. It appeared both in the Suram range (Caucasus) in a moist, mild, sub-alpine climate, and in the Don region in a warm, relatively dry and continental climate. In both cases the plants were constant (hereditary) forms from the beginning.

We shall now consider a few examples of a determined course in evolution.

2. FACTS FROM COMPARATIVE MORPHOLOGY

1. In the kingdom of plants, beginning with mosses, and continuing with ferns and gymnosperms, we observe a gradual reduction of the sexual (gametophyte), and a corresponding increase in the importance of the asexual (sporophyte) generation. Notably the ferns (Pteridophyta, to which belong the classes of true ferns, horse-tails, Isoetales and club-mosses) clearly show a determined course in their development, which leads them on in the direction of seed-plants (gymnosperms and angiosperms).

In terrestrial ferns and horse-tails, we still see a well-developed sexual generation in the shape of a prothallus, supplied with rhizoids and consequently self-supporting.

[1] "Life and Letters of Charles Darwin," ii, 1888, pp. 231, 232.

In the heterosporous ferns (Marsiliaceae, Salviniaceae) and in the heterosporous club-mosses (Selaginella), on the contrary, the prothallus (gametophyte) is reduced ; it does not leave the integument of the spore and develops very few archegonia and antheridia, sometimes even only one of either. Thus, the megasporangium of Marsilia, a homologue of the nucellus of the ovule of the flowering plants, contains but one megaspore ; it gives rise to a female prothallus, which does not leave the megaspore, and develops only one archegonium. The germinating microspore of Marsilia, homologous with the pollen-grain of the flowering plants, contains a male prothallus of two antheridia and six sterile cells. In Selaginella and Isoetes, the rudiments of the prothallus, both male and female, are colourless (do not contain chlorophyll), and consequently are unable to nourish themselves. The reduction of the gametophyte here attains its extreme limit in the Pteridophyta. A step more, and we obtain the sporophyte of the gymnosperms, *which assumes reproductive functions.* The spike of Selaginella, with its megasporangia and microsporangia, may be fully likened to the flower of the angiosperms : the leaves carrying microsporangia correspond to stamens, and those that carry megasporangia to carpels. Goebel (1915), indeed, speaks of the spike of Selaginella as a flower. The structure of the young microsporangium in Selaginella is wonderfully like that of the pollen-sac of the dicotyledons.

It is extremely significant, although not yet widely known, that *Selaginella rupestris* and *S. apus* have *a kind of "pollination"* (according to the investigations of F. Lyon, 1901). In *S. apus* the microsporangia situated above shed their microspores on to the megasporangia lying below, while the latter *are still attached to their spikelets, i.e.* to the plant itself. In the meantime archegonia have been formed in the megasporangia. If rain falls, or dew, the integument of the microspore, within which the rudiment of the prothallus has previously been formed, bursts, and the spermatozoids emerge and fertilise the archegonium. *The entire process of fertilisation thus takes place on the sporophyte, as in the higher plants.* After fertilisation, the spikelet is shed, and the young sporophyte germinates freely, between the sporophylls.[1] In

[1] On this subject see Lotsy, ii, 1909, p. 493.

S. rupestris the sporangium with the embryo becomes surrounded by a peculiar outgrowth of the sporophyll, which recalls the *integument of the ovule* in seed-plants. Consequently, in certain species of Selaginella we see the beginning of the formation of *seeds*. Finally, seed-like structures occur in two fossil club-mosses, Miadesmia and Lepidocarpon. We do not mention seed-" ferns " (Pteridospermae), because they are now referred to true gymnosperms.

We may thus trace the entire process of the reduction of the gametophyte, commencing with its flourishing condition in mosses, and proceeding with its gradual decline in the Pteridophyta, until we come to its complete disappearance in gymnosperms and its final replacement by the sporophyte in angiosperms. A definite course of evolution is here strikingly exemplified.

It might seem that in all the foregoing we encounter separate links of one genealogical chain : that the Pteridophyta are derived from mosses (Bryophyta), and the gymnosperms from the heterosporous Pteridophyta resembling Selaginella. But such is not the case : Bryophyta and Pteridophyta are apparently two independent parallel branches. Mosses and liver-worts, says Bower in his " Origin of a Land Flora " (1908), most probably are terminal branches of development ; the same opinion is shared by Meyer (1916, pp. 36-37). The ferns, says Gothan, are much older than the mosses ; the oldest land-plants we know show characters of the Pteridophyta, and the recently-discovered Rhynia and Hornea, of the Lower and Middle Devonian, are the most primitive Pteridophyta, allied to the club-mosses of the order Psilotales (Potonié, 1921, p. 480). The gymnosperms have not been derived from the heterosporous Pteridophyta. The most primitive gymnosperms, or so-called " seed-ferns " (Pteridospermae or Cycadofilices) derive their origin, so think Lotsy (ii, 1909, pp. 706, 729) and Berry (1920, p. 339), from the Palaeozoic ferns Primofilices, allied to the recent Marattiales, *i.e.* to the isosporous ferns. Wettstein (1911) also regards the ferns Eusporangiatae (to which, among recent forms, the primitive Ophioglossaceae and Marattiaceae are referred) as the ancestral *forms of gymnosperms, rejecting the suggestion as to the* origin of gymnosperms from heterosporous club-mosses.

The Lycopodiales, says Berry (1920, p. 334), are not related to any of the higher seed-plants, and never gave rise to more highly organised types. D. H. Scott even asserts (1923, p. 59) that seed-plants (*i.e.* gymnosperms + angiosperms), of which the pteridosperms are among the earlier representatives, constitute *an independent phylum* of equal antiquity with any of the recognised lines of vascular cryptogams. "Although the homologies of the reproductive organs in seed-plants and the higher spore-plants can, to a considerable extent, be traced, there is nowhere any indication of a transition from one to the other" (p. 52).

A definite course of evolution, which may be traced from Pteridophyta through gymnosperms to the angiosperms is thus manifested in various genetic branches, thereby adding weight to the importance of the orthogenetic process.

2. The comparative anatomy of animals supplies a number of striking examples of a definite direction in evolution. Among vertebrates we may mention the evolution of teeth in reptiles and mammals, the gradual ossification of the vertebral column (Fig. 11), a reduction in the number of the bones of the skull, the transformation of a two-chambered heart into a three- and four-chambered organ in connection with a corresponding complexity in the circulatory system, the evolution of the brain. We are unable to treat fully of all these cases, for the whole subject of comparative anatomy literally bristles with facts exemplifying development in a definite direction. We will, therefore, confine ourselves to a few cases.

Osborn (1902, 1907), basing his inferences on the study of the *teeth* of various groups of mammals, comes to the conclusion that teeth have "predispositions" to vary in a definite direction: in the process of the evolution of teeth full development is reached only by what had previously existed in a potential condition. Therefore, similar characters in teeth appear quite independently in various groups, such as horses, rhinoceroses, Titanotheria.[1] Nor

[1] The Titanotheria form a sub-order of the Perissodactyla.

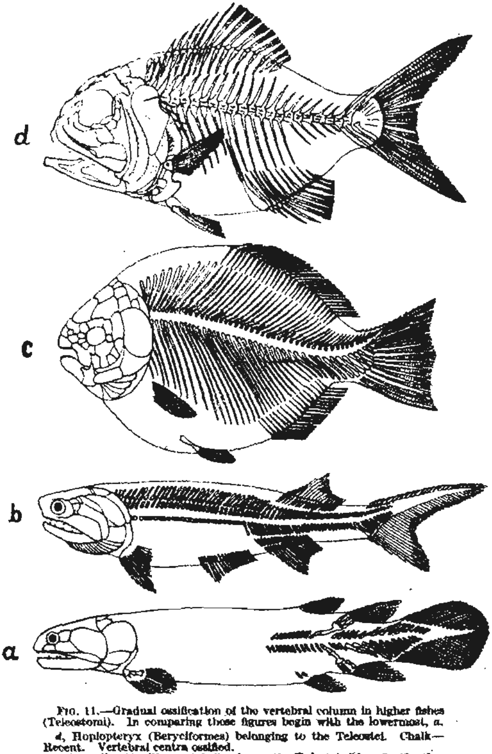

FIG. 11.—Gradual ossification of the vertebral column in higher fishes (Teleostomi). In comparing these figures begin with the lowermost, *a*.

d, Hoplopteryx (Beryciformes) belonging to the Teleostei. Chalk—Recent. Vertebral centra ossified.

c, Dapedius (Amiiformes) belonging to the Holostei. Lias. Ossification proceeds further, but vertebral centra not ossified, notochord persisting.

b, *Palaeoniscidae*. *Carboniferous, Permian*. Whole vertebral column ossified, but no vertebral centra.

a, Crossopterygii. Devonian. Vertebral column ossified in its posterior part, where only upper and lower arches are bony.

(From O. Abel, "Die Stämme der Wirbeltiere." Berlin and Leipzig, 1919. "Vereinigung wissenschaftlicher Verleger." Walter de Gruyter & Co.)

is this all. It is possible to detect a similar evolution of the tubercles of the molars in such widely separate groups as Perissodactyla and Primates (including the Lemuroidea). Tubercles appear in a strictly definite position, so that here there can be no question of chance. We have to deal here, says Osborn (1902, p. 267; 1907, p. 228), with a definite and determinate evolution, governed by certain rules. This may be seen from the following (Osborn, 1902, pp. 267-268; 1907, pp. 235-236):—

1. Teeth are distinguished by a very singular property, *i.e.* that they are laid down and formed *under the gums*. Consequently, use or disuse cannot exert any effect upon their form. On the contrary, the more they are used, the sooner they wear out.

2. At the same time, teeth are one of the most progressive organs.

3. The different families and orders of the Mammalia diverged from one another at the time when their upper molars possessed three tubercles each, the lower from three to five. Therefore, only those tubercles are homologous which may be compared to the above-mentioned primary ones.

4. New supplementary tubercles are consequently not homologous, but convergent. At the same time *the occurrence of such tubercles is independent of individual variation.*

Natural selection could thus play no part in the evolution of teeth in mammals, because they appear in perfectly definite positions.

Had the supplementary tubercles appeared without any definite order, at random, we should then have observed an unusual diversity in the teeth of mammals in all parts of the world. But such is not the case: as we have seen, the occurrence of new tubercles follows definite rules in various families; in the upper molars from one to eight supplementary tubercles develop at strictly definite points.[1] We thus unavoidably come to the conclusion that even in the primary trituberculur condition of the molars a tendency has been inherent which to a certain extent predetermines their future variation and evolution (1907, p. 237).

[1] Osborn, 1902, p. 268; 1907, pp. 228, 236.

Not only do the teeth, says Osborn, develop independently of chance variations being selected (for tubercles are predetermined); but the skull, the vertebral column and the extremities are subject to the same principle of development in a definite direction (1907, p. 237).

The four-chambered *heart* has been developed in crocodiles, birds and mammals quite independently. The growing complexity of the heart in the series of vertebrates exhibits, in general, a perfectly definite direction—from the two-chambered heart of fishes, through the three-chambered organ of amphibians and the majority of reptiles, *to the four-chambered heart of crocodiles, birds* and mammals.

Yet in the dipnoan fishes a tendency is shown towards the transformation of a two-chambered into a three-chambered heart; from the ventral side rises a septum partially dividing the auricle into two halves, the right and the left, and during the contraction of the heart a complete separation of the auricles is effected. But the same is quite independently foreshadowed in the teleostean fish Gymnarchus (of the family Gymnarchidae, allied to the Mormyridae), which possesses a cellular air-bladder (Assheton, 1908). *Although* the auricle in the amphibians is divided by a septum, the latter is perforated; in certain Salamandridae the lungs are completely reduced and the auricle has no partition wall. In reptiles the auricles are completely separated: in lizards, snakes and tortoises a tendency to separate the ventricle into two halves is manifested; there is a septum, which, however, remains incomplete, and only in certain forms (Varanus), during the systole, a complete separation between the two halves of the ventricle is attained. Finally, the ventricle is also completely partitioned in crocodiles, birds and mammals. In crocodiles, however, the arterial blood of the right arch of the aorta comes into communication (although in an insignificant degree) with the venous blood of the left through the foramen Panizzae. In birds and mammals, the total separation of the current of the arterial from that of the venous blood has become complete.

The comparative anatomy of the heart in vertebrates thus strikingly exemplifies development in a definite direction. But with this or that structure of the heart is

connected the entire organisation of the circulatory system and of many other organs of the first importance.

Let us trace the evolution of the *arterial and venous systems* in vertebrates. Beginning with lampreys and fishes and ending with mammals, the number of pairs of aortic arches steadily diminishes. Their primitive number should correspond to the number of gill-clefts. The embryos of the Selachii possess six. In all Tetrapoda the first and second pairs of arches disappear, and in the salamander four are met with; as in amphibians and reptiles, so in birds and mammals the fourth pair of arches gives rise to the aorta. In amphibians and reptiles the right and left arches of the fourth pair are transformed into the roots of the aorta, the latter thus possessing two roots (aortic arches); birds and mammals have only one aortic arch each, birds the right arch and mammals the left. The fifth pair is found only in tailed amphibians and certain lizards, while the sixth remains in tailed amphibians in the shape of a third pair of aortic arches, becoming pulmonary arteries in the other vertebrates.

In this case also a determined direction in evolution is made strikingly evident: what is especially deserving of notice is the identical result reached by birds and mammals in the development of the arches in various ways and quite independently.

The development of the *urino-genital system* in the males of fishes is directed towards the dissociation of the efferent ducts of the testis from any connection with the mesonephros. All the stages of the process may be observed in the Dipnoi, beginning with Ceratodus and ending, through Lepidosiren, with Protopterus, in which each testis is connected with only *one* mesonephridial canaliculus. But the same process of loss of connection between the male genital and urinary organs is accomplished quite independently in Holocephala, Polypterus, the Teleostei (in the narrow meaning of the term, without the Holostei) and, lastly, in some of the Anura (tailless Amphibia).

A determined direction may also be seen in the gradually growing complexity of the *brain* (Fig. 12). It is a remarkable fact in the anatomy of crocodiles and birds that the resemblance they exhibit in the heart is also

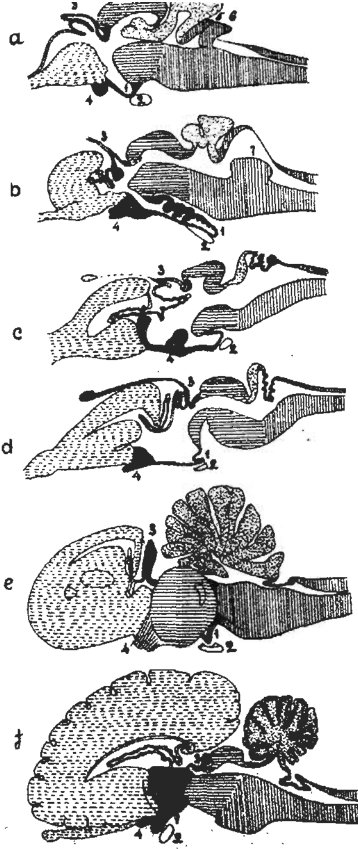

FIG. 12.—Gradual complication of the brain. Diagrammatic longitudinal sections. *a*, bony fish; *b*, electric fish (Torpedo); *c*, frog; *d*, reptile; *e*, bird; *f*, mammal. Horizontal interrupted lines represent the fore-brain; dark netting—diencephalon; horizontal lines—mid-brain; vertical lines—medulla oblongata; dots—cerebellum. (From Hesse and Doflein, "Tierbau und Tierleben," II. 1914. Teubner, Leipzig.)

manifested in the structure of the brain. The hippocampus first appears in the Dipnoi and Gymnophiona, and then in all the vertebrates, from reptiles onwards, gradually acquiring an ever-growing complexity. The *same gradual complication we see in the structure of the* hemispheres of the brain, of the cerebellum, etc.

If such complicated systems as the osseous, circulatory and nervous are perfected through the effect of inner causes, without any intervention on the part of selection, it would seem quite useless to resort to selection for the explanation of the origin of such simple structures as external characters.

In face of such facts, how can the chance occurrence of characters be maintained? How small must be the probability in the series of vertebrates of the *chance* occurrence, in the very nick of time, of characters which would contribute *step by step to the transformation of the two-chambered* heart into a four-chambered organ, these characters being the whole time strictly coordinated with modifications in the circulatory system, in the organs of respiration and in the muscles!

3. FACTS FROM PALAEONTOLOGY

In all the research since 1869 on the transformations observed in closely successive phyletic series no evidence whatever, to my knowledge, has been brought forward by any palaeontologist, either of the vertebrated or invertebrated animals, that the fit originates by *selection from the fortuitous.*

H. F. Osborn, 1909, p. 223.

One of the most interesting cases of development in a determined direction is afforded by the deer. Different species of the Miocene Palaeomeryx lead quite independently through the genera Dicroceros and Cervavus to the genus Cervus.

The genus Cervus thus appears to be polyphyletic. But polyphyletic development is irreconcilable with the principle of selection, as it excludes the operation of chance in the production of characters. Every polyphyletic genus affords *most obvious evidence in favour of the assumption that*

development follows a definite course, that it could not proceed in any other way than the one it has taken, that variations are not infinite, but strictly limited in number, and that polyphyletic evolution is not the exception, but the rule.

Many palaeontologists assert that the horses (Equus) of the Old and New World developed polyphyletically; in North America in the Pleistocene time from forms similar to Pliohippus (Upper Miocene-Lower Pliocene) and Merychippus (Middle Miocene-Lower Pliocene), while in Europe they owe their origin to Hipparion, namely, to *H. minus* (Antonius, 1919, p. 292). The genus Equus has thus been derived independently in Europe and America from two different genera. But as other authors hold a different opinion on the subject (applying the theory of migrations), we shall not go further into the matter. We may mention, however, that Abel (1919, p. 864) thinks he is able to get out of the difficulty by establishing a new genus Neohippus for the Pleistocene horses of America.

Another remarkable case of a definite direction in evolution is afforded by marine sirenian mammals, belonging to the fossil genus Metaxytherium (from the Miocene and Pliocene). In the Oligocene of Europe lived *Halitherium schinzi*. In various parts of Europe this species gave origin to new species, which have all varied *in a definite direction*: Abel (1909) counts eighteen characters, which have all similarly varied when compared with *Halitherium schinzi*; in all are observed enlarged and more complex molars, broader and larger scapulae, a strengthening of the points of attachment of the muscles to the humerus, or elongation of the metacarpalia, a reduction of the pelvic and nasal bones, etc. The presence of so large a number of common characters has led to the grouping of all these new species in one separate "genus," Metaxytherium, which is remarkable for the fact that all its *species have arisen independently of one another, in different places, from various ancestors.*

We may further note the gradual reduction of the hind limbs and the pelvis in the series of aquatic mammals,

Cetacea and Sirenia. In the Sirenia, according to Abel's researches (1912, p. 191), the following series may be noted (see Fig. 13). *Eotherium aegyptiacum* Owen, from the Middle Eocene of Egypt, has a well-developed acetabulum; the animal, therefore, must have had functional hind-limbs. But the obturator or ischio-pubic foramen is closed anteriorly by a thin wall, which feature indicates an incipient reduction of the pelvis. In *Eosiren*

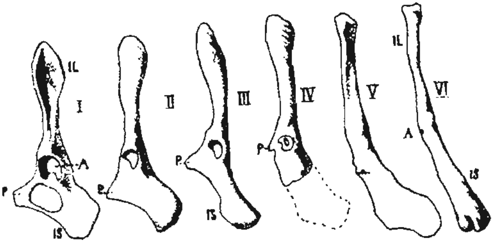

FIG. 13.—Reduction of pelvis in Halicoridae (Dugongs). Note the gradual reduction of the pubis, which is entirely wanting in Halicore, the pelvis consisting only of the ilium and ischium. Simultaneously the acetabulum becomes reduced.
(From O. Abel, "Die Stämme der Wirbeltiere." Berlin and Leipzig, 1919. "Vereinigung wissenschaftlicher Verleger," Walter de Gruyter & Co.)

libyca Andrews, from the Upper Eocene, the acetabulum has become so small as to imply the atrophy of the hind-limbs; the obturator foramen is absent; the pubis is little developed. A further stage in the reduction of the pelvis is manifested in *Halitherium schinzi* Kaup from the Middle Oligocene. In the Middle Miocene Metaxytherium the pubis is represented by a mere vestige. In *Halicore dugong*, now living, the pubis and acetabulum have entirely disappeared.

A completely parallel series of stages of atrophy is observed in the Cetacea (Abel, 1912, pp. 194-196).

The evolutionary series of horses, leading from the Eocene Orohippus, through Mesohippus (Oligocene), Miohippus (Miocene), Protohippus (Pliocene), Pliohippus (Pliocene) to the recent Equus is known to every zoologist.

In the series of horses the dental system is developed in such a direction that in the ancient forms the widest tooth belongs to the molars, and as the more recent forms are approached the maximum width is gradually transferred to the premolars. Thus, in the Lower Eocene North American horse *Eohippus cristonensis* the widest tooth is the second or third molar. In the Middle Eocene *Orohippus uintanus* the widest is the second molar, in the Upper Eocene *Epihippus uintensis* the first molar, in the Lower Oligocene Mesohippus the fourth premolar; in the Upper Miocene Hypohippus the third or fourth premolars are practically of the same size. In the Pleistocene *Equus complicatus* the widest are the third and fourth premolars, and in the living *Equus caballus* the third premolar (Granger, 1902, p. 262, Fig. 5).

The evolution of the true crocodiles (Eusuchia) follows the direction of the transformation of forms with platycoelous and amphicoelous vertebrae into forms such as the now living Gavialidae and Crocodilidae, with procoelous vertebrae. A tendency is also observed to shift the choanae, or internal nasal apertures, backwards: in the ancient forms they open behind the palatines; in the more recent (beginning with the Cretaceous period) the choanae, as in the existing forms, are surrounded by the pterygoids. Finally, beginning in the Jurassic, a disposition may be observed to surround the eustachian tube with a bony case.

In four or five different groups of Titanotheria may be observed a tendency towards a definite localisation of the horns, and their evolution in a determined direction (Osborn, 1912, p. 253). The rudiments of horns appear in the form of inconspicuous protuberances at the very same points on the skull in representatives of the various groups of Titanotheria in various geological periods, and these rudiments subsequently develop into very conspicuous structures. They first become apparent in the adults, and continue then to be formed in ever younger Titanotheria, until, finally, they are present in the embryos.

The development of the Nautiloideae proceeds in the direction of a transition from forms with a straight shell to those with a spiral one; all the branches of this stem pass through the stage formerly known as the genus

Cyrtoceras. In calling attention to this case, Dacqué (p. 67) says that, if the survival of the spiral forms, as being undoubtedly the more progressive, be attributed to selection, the entire group must have then become extinct, as unfit, before the formation of the spiral forms had commenced. Moreover, during the Carboniferous and Permian periods we see in various branches of the Nautiloideae alongside the spiral forms a recurring production of straight-shelled forms, which would seem, on that supposition, to have been doomed to extinction.

According to Grabau (1907, p. 621) all the characters in the shell of gastropods appear in a definite order, and develop by a process of progressive intensification or growth. The type of the hinge in Trigonia has been prepared in the Devonian, is further evolved in the Lower and Middle Triassic, and in the Upper Triassic attains its final form, which it still retains (Jaekel, p. 19).

So long ago as 1866 Hilgendorf described the transformations occurring in the Upper Tertiary mollusc *Planorbis multiformis* throughout a successive series of deposits. His inferences were contested by Sandberger and others, who maintained that Hilgendorf had dealt with the evolution, not of one form, but of various genera and species, which had simultaneously existed in the same basin. The most recent investigations (Gottschick, 1920) have fully confirmed the correctness of Hilgendorf's opinion. At Steinheim (Würtemberg) in the upper deposits of the Upper Miocene may be observed a very rich fauna of pond Mollusca. Here, among others, may be found *Planorbis* (*Gyraulus*) *multiformis* in three forms (*applanatus*, *dealbatus* and *kleini*), *Limnaea* (*Radix*) *dilatata*, *Pseudamnicola pseudoglobulus*, and many others. In the course of time the hydrographic conditions of the basin became modified, and traces of the subsequent presence of hot springs have been found; with these the rich antecedent fauna disappears, with the exception of the above-mentioned species. In the successive deposits of the hot springs *Pl. multiformis* experiences a peculiar evolution, giving rise to a series of forms: the shell increases in size and becomes thicker, while in other forms it again becomes smaller. In Plate's (1920) opinion, we here meet with a "rare case" of evolution in a definite

direction, without any intervention on the part of natural selection; in the successive transformations all the individuals took part ("so gut wie alle Generaticnen an diesen Veränderungen teilnehmen": Plate, 1920, p. 218): nothing can be adduced in favour of the slight differences in the size and the sculpture of the shell having had a selective importance. These inferences of Plate are perfectly correct; but his opinion, that the type of evolution of *Pl. multiformis* is exceptional or rare, is not correct: all evolution is of the orthogenetic type.

4. ONTOGENY

> ... *dass die Entwicklung der einzelnen Organismen nach denselben Gesetzen* geschicht, als die der Tierreihe, d.h. dass das höhere Tier in seiner Entwicklung, dem Wesentlichen nach, die unter ihm stehenden Stufen durchläuft.
>
> F. Meckel, "System der vergleichenden Anatomie," i, *Halle*. *1821*, p. *396*.

If, setting aside preconceived theories, we regard things from a rational point of view, there can be no better refutation of the theory of selection than the individual development of the organism, or, as it is called, ontogeny. As regards the embryo, it is scarcely possible to speak of the struggle for existence, for Nature has surrounded it with the most favourable conditions, especially in placental mammals, viviparous sharks and other viviparous animals. And we see, in fact, that in vertebrates embryonic development at first always follows a definite direction: first appears the blastopore or the primitive streak, the central nervous system is then formed, subsequently the notochord, the somites, and after a time in all vertebrates appear the visceral arches, etc.[1] *All this serves to show that the course* of development is subject to a certain law. The presence of branchial arches in the embryo of man is no proof that man in his phylogenetic *development has at some time passed* through the stage of a fish; it simply shows that, in mammals, in certain conditions of embryonic development,

[1] In the lampreys and in the *Marsipobranchii* in general, however, the branchial arches develop in a very peculiar manner.

an organ resembling the branchial arches of lower vertebrates *must* be formed.

In so far as the conditions of development are the same and the diversity of the original material permits (for, as O. Hertwig justly remarks, the ovum of the bird differs as much from that of man as do the adult animals), embryonic development is cast in approximately similar forms. Ontogeny repeats phylogeny, not because the organism had passed through the same stages that are manifested in ontogeny, but for the same reason that parallel branches develop in the same direction: *at a certain period of development*, both in the embryo of the fowl and in that of man, a *notochord and* branchial arches are met with, just as in dinosaurs and birds similar features in the skeleton and the *organs of respiration are encountered*, although *birds were* at no time derived from the dinosaurs.

Therefore, the definition of the "biogenetic law" as given by O. Hertwig (1888) is perfectly correct: it is a repetition of forms obeying the laws of organic development and following the path which leads from the simple to the complex.[1] *All* ontogeny, or individual development, represents, not a repetition of the past, but, on the contrary, as Baer pertinently remarks (1876, p. 456), *a preparation of future stages by the aid of preceding ones.* It is the highest embodiment of the principle of development in a definite direction, *i.e.* of development *determined by law.*

Indeed, what is "law" in natural science? In observing Nature we detect a *sequence* of phenomena and a *connection* between them, which consists in the repetition of the same phenomena when the same conditions recur. The probability of the future occurrence of such a repetition we call law. New characters, both in the course of ontogenetic and phylogenetic development, arise not at random, but in a

[1] Cf. on the same subject: Baer, 1828, p. 190; Keibel, 1898; Vialleton, 1911, pp. 735-749; O. Hertwig, 1916, pp. 185-234, 1920, pp. 740-749. See also T. Morgan, 1903, pp. 58-83; Eimer, 1897, p. 23.

certain sequence and in such a manner that, knowing the preceding stage, we may foretell the following; or, in the words of Baer, the preceding stage prepares the future one. Briefly, the development of the organic world is a process determined by law. One of the manifestations of such a compliance with law is heredity.

As ontogeny not infrequently anticipates future forms (see chap. ii), it may therefore not only "repeat," but also "anticipate" phylogeny. Therefore, it would be incorrect even in this sense to view ontogeny as a repetition of the past. With as much justice it could be said that the adult stages of lower forms anticipate and imitate the young stages of higher forms, as, in the branchial apparatus, adult fishes anticipate what will be subsequently realised in young amphibians or reptiles (in that very sense the so-called biogenetic law was formulated by Cope as early as in 1871 [1887, p. 175]: "It is well known that in both kingdoms, in a general way, the young stages of the more perfect types are represented or imitated with more or less exactitude by the adults of inferior ones").

We may summarise the present section in the following words: the laws of the organic world are the same, *whether we are dealing with the development of an individual* (ontogeny) *or that of a palaeontological series* (phylogeny). Neither in the one nor in the other is there room for chance.

5. ONE OF THE METHODS BY WHICH CHARACTERS ARE FORMED

We shall now take a few instances to illustrate *one of the ways* in which new characters are formed, and which is effected by internal causes. In the formation of all the characters of which we shall treat below, selection plays no part: they are all produced in a determined direction.

"Flight" of Fishes. On the origin of the capacity for "flight" in fishes, Abel says (1912, p. 320; cf. also 1906, p. 86) that the capacity for flying in Dactylopterus (a fish

of the order Acanthopterygii and of the group Cataphracti) may be explained by one supposition, namely, that the ancestors of this fish inhabiting the bottom of shallow waters, while escaping from their enemies, were in the habit of leaping and were occasionally carried right out of the water. The large fins of this fish while in the air acted as parachutes. Owing to repeated use these fins became more and more adapted for flight.[1] In much the same manner, according to Abel, has been developed the faculty of flight in the pelagic fish Exocoetus, belonging to quite a different group, namely, to the order of Beloniformes.

We must first of all observe that, with regard to Dactylopterus, its ability to "fly" has not yet been finally established. And, in general, the term "flight" here must not be understood too literally. The true "flying" fish Exocoetus leaps out of the water and, in consequence of the impetus acquired, continues to move above the surface for a distance of several hundred metres without making any motion with its pectoral fins. It is unable to change a direction once acquired.

Möbius (1878), as may perhaps be known, has asserted that flying-fishes are unable to move their fins during flight. Seitz (1891), a very intelligent observer, says, on the contrary, that he not infrequently saw the fluttering of the pectoral fins during the flight of the flying-fish. He describes the process in the following manner (p 364-365): by means of the lateral musculature of its body the fish leaps out of the water; it helps itself by bringing its pectoral fins into rapid motion, the range of the strokes for a fish 20 cm. long attaining as much as 10-12 cm.; having, while leaping out of the water, reached its greatest altitude, it spreads out its fins horizontally or, more often, raises them, and then continues its flight as if sliding down a declivity without moving its fins, but employing them as parachutes; if the fish has to rise

[1] Cf. also Darwin's "Origin of Species" (chap. vi, p. 140): "It is conceivable that flying-fish, which now glide far through the air, slightly rising and turning by the aid of their fluttering fins, might have been modified into perfectly winged animals."

again above the water, the fins are again brought into rapid movement. Thus in the ascending part of the curve of flight, according to Seitz, the fish moves its fins while in the sloping descent it does not. The number of vibrations of the fins he estimates at 10-30 a second (p. 372), the distance flown by the fish at about 400 metres. Dahl (1891), while not denying the accuracy of Seitz's observations, remarks that Exocoetus is able to perform movements with its pectoral fins only when its *tail touches the water; in the air the fish is unable to move its fins.* Having flown some distance above the water, the fish descends and dips its tail into the water: at this instant the fins again begin to flutter rapidly, and the fish rises anew and flies further; this takes place over the waves' crests (p. 681). One old observer, Bory de St. Vincent (1804), very aptly compares the flight of the flying-fish with the movement of a stone, which, being thrown along the water's surface and rebounding again and again, repeatedly rises above the water. The above has been confirmed by so many witnesses that the matter may be now considered as finally established.

The flying-fish, consequently, does not move its fins in the air.

Again, the elongation of the fins is met with not infrequently in fishes that exhibit no propensity for flying.[1] Thus, in the fish *Pterois volitans* (L.) of the Scorpaenidae, belonging, with the Dactylopteridae, to the same group of Cataphracti, all the fins, especially the pectoral and dorsal, are very much enlarged, whence its specific name "flying," although the fish shows no disposition to fly: it is found in fissures of coral reefs. Further, in the North American fish *Prionotus evolans* (L.) of the family of gurnards, Triglidae, (allied also to the Dactylopteridae) found on the coasts of North and South Carolina, the pectoral fins are much elongated, much more so than in the European gurnard

[1] In the fossil fish *Chirothrix libanicus*, Pictet et Humber, 1866 (Upper Turonian of Lebanon; in a related form, found in the Upper Cretaceous of Westphalia), and belonging to the Chirothrissidae, the ventral (not pectoral) fins are very much enlarged. This fish, it would seem, was not able to fly. The ventral fins are similarly enlarged in the pelagic fish Gastrochisma (Scombridae) now living. (See Abel, 1906.)

(Trigla), although this fish, being a bottom fish, does not, of course, fly. All the above are examples of a normal elonga-

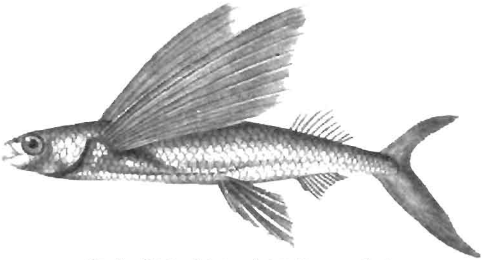

FIG. 14.—FLYING FISH, *Cypselurus californicus*. Pacific. (From D. S. Jordan, "A Guide to the Study of Fishes." New York, 1905. D. Appleton & Co.)

tion of the pectoral fins. But among fishes not infrequently occur cases of a pathological enlargement of fins, chiefly the pectorals. In 1916 I described a specimen of the Aral Sea roach with extremely elongated pectoral (and other) fins,

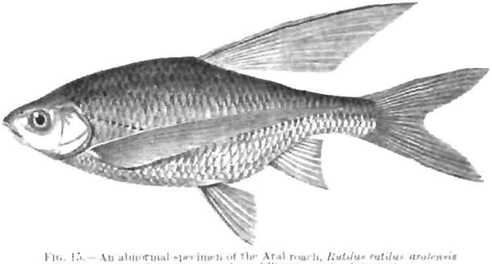

FIG. 15.—An abnormal specimen of the Aral roach, *Rutilus rutilus aralensis* monstrositas *exocoetides*, with fins enlarged like those of a flying-fish. (After L. Berg, original.)

under the name *Rutilus rutilus aralensis* monstrositas *exocoetides*. Similar monstrosities were previously known

in the perch (from the Yenissei) and in the tench (*Tinca tinca*) and the barbel (*Barbus barbus*) from France. While studying the question of the origin of similar monstrosities, I suggested that possibly in this case we meet with a phenomenon analogous to acromegaly in man. As is known, this affection is caused by the hypertrophy or swelling of the pituitary gland. In the American gurnard, *Prionotus evolans*, mentioned above, the pectoral fins normally reach somewhat beyond the middle of the body, but sometimes specimens occur with very much elongated pectorals, which may reach nearly to the base of the caudal fin (Jordan and Evermann, ii, p. 2168).[1]

If we imagine that, through the effect of some (internal or external) causes, the inner secretion of the pituitary gland should increase and continue so during life, as a consequence an enlargement of all the fins must then follow, quite independently of use or disuse. As the composition of proteids in allied forms is similar, it is quite conceivable that in allied forms, such as the representatives of the families Scorpaenidae, Triglidae and Dactylopteridae, fins should be elongated.

But how did flying originate? Very many fishes have a tendency to leap out of the water, either in saving themselves from enemies, as in the case of many fresh-water fish in the Volga in their escape from *Aspius aspius* (Aleksandrov), or in a state of sexual excitement (as in the Acipenseridae), or, lastly, in a paroxysm of fear. V. K. Soldatov tells me that in the lakes of the lower Amur the tolpyga, *Hypophthalmichthys molitrix*, a fish of the carp family, reaching seven pounds in weight, on being frightened by the noise of oars or of a motor-boat, leaps out of the water and not infrequently drops into the boat by dozens, sixty to seventy at a time. It leaves the water at an oblique angle and may rise to the height of ten feet above the surface. Its pectoral fins,

[1] In this connection it is interesting to note the following passage from Darwin's "Origin of Species" (chap. ii, p. 34): "I have as yet failed to find, after diligent search, cases of monstrosities resembling normal structures in nearly allied forms." See also below, chap. v.

however, are not *elongated*. In general, many fishes with a strong tail musculature, such as salmon, are able to leap out of water. The minnow (*Phoxinus phoxinus*) in the Alps leaps from one pool to another over intervening ridges of gravel, and the Siberian *Phoxinus percnurus*, according to some observers, in jumping out of the water, reaches a height of seven feet or more.[1]

If, therefore, fishes with *non-extended fins* may "fly," there is nothing surprising in the fact that a fish possessing such a parachute as is represented by the fins, say, of Exocoetus, is capable of remaining a considerable time in the air. What may be the purpose of such flight it is difficult to say. Possibly it is as much a reflex as that of the tolpyga, which is due to fright.[2] It may be possible, however, that *flight is of use to the fish, enabling it to escape from its pursuers*. But it is clear from the preceding that, in the modelling of the form of the fins, the act of flight, in spite of Plate's opinion ("Selektionsprinzip," p. 141), has played no part. And if the fish has made use of its pectoral fins for a definite purpose, that is a matter of instinct, *i.e.* *skill*, psychical adaptation.

If it be true that the increase in the size of the pectoral fins is a consequence of a more vigorous secretion of some organs, cases of the opposite condition, *i.e.* a reduction in *the size of the fins due to a diminished secretion, might be* expected to occur. And, as a matter of fact, such cases have actually been observed. In many South American species of the family (or, to be more correct, in the group of families) Characinoidei, individuals occur with rudimentary pectoral fins, and this although the species belong to genera very widely separated from one another in the system, *i.e.* in those which are grouped about Nannostoma, Tetragonopterus, Characinus (Eigenmann, 1912, p. 108). Cases of

[1] See on this subject my "Fishes" (in "Faune de la Russie"), iii, part i, 1912, pp. 262-263.

[2] Exocoetus, like the tolpyga, also drops on the deck of passing vessels.

such anomalies referring to several species of the genus Hyphessobrycon (of the Tetragonopterus group) have been described. One of the Guiana species of that genus possessing the anomaly in question has even been described as a separate genus, Dermatocheir (*l.c.* p. 343). The same has happened to a species of a distantly related genus, Poecilobrycon, which gave origin to an imaginary new genus, Archicheir, with the species *A. minutus* Eig. (*l.c.* p. 287).

Possibly, by the same means may be explained the normal absence of pectoral fins in some fish, as in some genera Stomiatidae.

The example of flying-fishes shows us how a character may be formed as the effect of certain laws, without any intervention on the part of natural selection or of the use or disuse of organs. The elongated pectoral fins have been formed because their formation was *inevitable*.

Other instances. Many of the Psocidae, an order of insects which are grouped by some with termites, Embiidae and Mallophaga, have wings which are never used for flight, and sometimes are not even suitable for it. Many of these insects, according to MacLachlan, are so averse to flying that they will allow themselves to be crushed rather than take to flight. Some Psocidae are entirely destitute of wings; but, among the winged forms, some individuals, or even whole generations, possess rudimentary wings. The above instances induced the well-known entomologist Kolbe (1884) to say that, in the Psocidae, wings are present, not so much for flight, as because it is in the nature of these insects to possess those organs.

In disputing the assertion of Lamarckians that the use of organs always leads to an improvement of the latter and is a stimulus to further evolution, and that form is determined by function, Plate ("Selektionsprinzip und Probleme der Artbildung," p. 597) offers the following instance. In Fierasfer, a fish living inside holothurians, the vent is situated on the throat, "so that it has only to push its head out of its host's anus to rid itself of its excrements." In what manner, asks Plate, could the use of the intestine (let us say, its enhanced peristaltic action) involve such a

forward transference of the anus? From this passage it may be seen that Plate regards the anterior position of the vent as a *consequence of the adaptation to symbiosis* with the holothurian, which has been effected by means of natural selection.

But how much time must have elapsed before this adaptation could have taken effect by the means indicated? Can it be supposed that all that time the Fierasfer had amicably cohabited with the holothurian? There can be no doubt that the habits and mode of life of the fish would have altered in a much shorter period of time than that which would be required for such an adaptation.

It is obvious that the actual progress took an opposite direction, and this requires no strained explanation: the Fierasfer came to dwell in the holothurian, because its vent happened to be on its throat. With such a structure it was advantageous for it to do so.

In two different families of marine fish *sailing* fishes occur: in these fishes the dorsal fin attains such a length and is so high, that, by protruding it from the water, they use it as a sail, swimming with the wind. This has been observed to occur by such a competent authority as Weber (Siboga Exp., p. 408), who procured in the seas of the Malay Archipelago a specimen of *Histiophorus orientalis*, 2·68 m. long. But "sailing" fishes 5 m. long are occasionally met with, in which the dorsal fin is 1½ m. high. The genus Histiophorus belongs to the family Xiphiidae, closely allied to the mackerels (Scombridae). Another very distantly related family, counting sailing fishes among its members, is that of the Paralepidae; a member of this group, *Plagyodus* (*s. Alepidosaurus*) *ferox* (Lowe), reaches 2 m. in length and occurs in the Atlantic and Pacific Oceans. Dollo (1908) assumes that in both these "sailing" fishes the dorsal fin is an adaptation to the peculiar conditions of a nektonic life. But it is very difficult to conceive how the "sail" could be produced by means of selection. It is evident that the lofty sail of the "sailing" fish was formed in the same way as the elongated pectoral fins of the flying-fish, quite independently of selection. Being provided with such an organ, the fish used it as best it could. We may be sure that this innocent pastime, of swimming by means of the dorsal

fin, as though under sail, is of no use to the fish in its struggle for life, and affords it no superiority over its compeers which swim in the water in a normal fashion; the sailing fish, moreover, can do this quite as well as they.

The African egg-eating snake, *Dasypeltis scabra*, of the family Colubridae, sub-family Rachiodontini, feeds almost exclusively on birds' eggs. The teeth in the mouth cavity are rudimentary. In swallowing the eggs whole, the snake crushes them in the following manner: the lower spinous processes of (approximately) the first thirty vertebrae (not counting the two anterior ones) penetrate the wall of the oesophagus and protrude into its cavity (Kathariner, 1898, p. 516, plate 41). By these "oesophageal teeth" (and especially the processes of the 22nd-26th vertebrae) the eggs are crushed; their contents reach the stomach, and the shells are cast out through the mouth. Those who have written on this curious method of feeding [1] call it an adaptation of anatomical structure to nutrition.[2] I think, on the contrary, that in this case function is adapted to the structure of the vertebral column; there can be no doubt that the snake feeds in a not quite ordinary manner solely because its instinct enabled it to utilise the peculiar construction of its anterior vertebrae. The primary phenomenon was the presence of the vertebrae, their function was a secondary one.

That such is the case may be judged from the fact that in many snakes the spinous processes of the anterior vertebrae somewhat protrude into the cavity of the oesophagus, forcing the mucous membrane to bulge out (without perforating it); it is assumed (Rochebrune) that this is a contrivance to enable the snake to retain its prey within the oesophagus. There is another snake in which the lower spinous processes force in the wall of the oesophagus: it is the Bengalese ***Elachistodon westermanni***, belonging to the sub-family of Elachistodontini of the same family of Colubridae (but of another group, the

[1] M. Weber, M. Nussbaum, p. 433; Hilzheimer, p. 356, Fig. 223.

[2] Indications, based on the works of G. Saint-Hilare (1834), that "oesophageal teeth" of *Dasypeltis scabra* are said to be encased in enamel, are not infrequently met with. The investigations of Kathariner (1898, p. 507), however, have demonstrated that the lower spinous processes in the snake in question consist of osseous tissue, they possess neither dentine, enamel, nor cement.

Opisthoglypha); whether it feeds on eggs is not ascertained, but is considered likely (Rheinhardt, 1863). It is remarkable that in the mosasaurs, large Cretaceous sea-lizards (Lacertilia),[1] the cervical vertebrae were supplied with large lower spinous processes, which terminated in a peculiar tooth-like protuberance (especially conspicuous in the North American Upper Cretaceous *Clidastes*). In the group of Lepidosauria (lizards and snakes) we thus see a definite direction in the development of the anterior vertebrae, and their shape is no result of use or disuse; on the contrary, this also is a case in which function depends upon structure.

The reduction of the eyes in cave and subterranean animals was undoubtedly affected by the disuse of these organs. But they had previously shown a tendency towards the disappearance of eyes (Eigenmann, 1909, p. 13). It is known that the relatives of the cave species, which live in the open, not infrequently possess more or less reduced organs of vision, while some blind species dwell both in caves and in the open air. Six species of American blind or cave fishes, Amblyopsidae, always live in caves, and their eyes are reduced. One species, *Chologaster cornutus*, never inhabits caves, and yet its eyes show some reduction; in some respects the eyes are more degenerate than in the typical cave amblyopsid, *Typhlichthys subterraneus* (Eigenmann, 1909, p. 119). On the other hand, the American salamanders, *Spelerpes maculicauda* and *Sp. stejnegeri*, although inhabitants of caves, have normal eyes.[2]

Therefore, as regards many cave animals, there are grounds for assuming that they sought the dark because they were adapted to life in the dark or possessed a tendency towards blindness (Eigenmann, 1909, p. 13). "It is not the cave," says J. Loeb (1916, p. 326-7), "that made animals blind, but animals with a hereditary tendency towards a degeneration of the eyes can survive in a cave while they can only exceptionally survive in the open. The cause of the degeneration is a disturbance in

[1] They were formerly placed in a special sub-class, the Pythonomorpha.

[2] In connection with this subject we may mention the experiments of Payne (1910). He caused sixty-nine successive generations of the American fruit-fly *Drosophila ampelophila* to live in the dark, and yet could not discover any change in the organs of sight, or elsewhere.

the circulation and nutrition of the eye, which is as a rule independent of the presence or absence of light."

To the same class of phenomena of a determined direction in evolution may be referred the extremely peculiar and complex contrivances for fertilisation, which occur in the orchids, or for the capture of insects in the insectivorous plants. The flowers of orchids, a classical example of the doctrine of the origin of useful characters by means of the struggle for life, according to Detto (1904), scare, rather than attract, insects (de Vries, 1912). Regarding these same orchids, Neger (1913, p. 641) says, "as if evolution, led by some blind impulse, continues its course in certain phyla, according to a once acquired direction, ignoring all demands and being unable to lay out new paths."[1] De Vries further notes that the closed pollen-sacs of Mimulus and Torenia, described by Burck, though filled with pollen, are of no use to their possessors. The sundew (Drosera) in no respect predominates over the plants in the midst of which it grows, in spite of its capacity for capturing insects; on richer soils it may completely dispense with animal food. With reference to insectivorous plants, Neger says (1913, p. 344), "We cannot but wonder at the frequent insignificance of the result in these cases compared to the expenditure of force and matter. Nepenthes possesses unusually intricate contrivances for capturing animals, and yet the quantity of prey thus enticed is at times exceedingly small. In addition to which, the demand for animal food in some species of Nepenthes cannot be considered to be so very insistent, as they can very well thrive without it. It may be said, that in devising the traps for animal prey, the demand for that food provided, as it were, the impetus for developing in a definite direction, but therefore the same tendency has remained and continues to exist even in altered external conditions, quite independently of the true demands of the plant and of practical consequences. In

[1] "Eine Orchideenblüte mit ihren oft wunderbaren Einrichtungen zur Bestäubung, speziell Fremdbestäubung," says Goebel in his "Organography" (i, 1913, p. 32), "ist gewiss etwas sehr merkwürdiges. Wer aber nur vom Nützlichkeitsstandpunkt ausgeht, wird mit Recht fragen: wozu denn der ganze sinnreiche Apparat, während andere Pflanzen mit viel einfacheren Mitteln dasselbe erreichen? Offenbar ist das nur verständlich, wenn den Organismen das zukommt, was man früher 'Gestaltungstrieb' genannt hat."

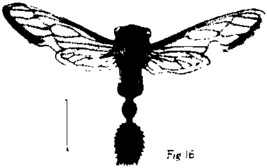
Fig 16

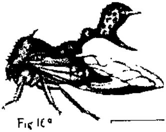
Fig 16a

Fig 17

Fig 18

Fig 19

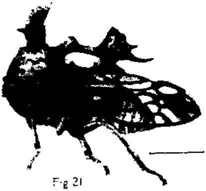
Fig 21

FIG. 16.—An ant-like membracid, *Heteronotus trinodosus*, male. Central America.

FIG. 16A.—An ant-like membracid, *Heteronotus trinodosus* female. Central America.

FIG. 17.—*Cyphonia clavata*. Central and S. America.

FIG. 18.—A fly-like membracid, *Parathonae dipteroides*. Guatemala.

FIG. 19.—*Sphongophorus biclavatus*. Central and S. America.

FIG. 20.—*Sphongophorus ballista*. Central and S. America.

FIG. 21.—*Smerdalea horrescens*. Guatemala, Panama.

(From W. Fowler, Hemiptera, in "Biologia Centrali-Americana. Quaritch, London.)

Fig 20

this way most remarkable organs have been elaborated which are none the less a luxury for the organism. A definite direction in evolution of this kind does not in any case accord well with the principle of selection—the survival of the fittest."

The Membracidae, a family of Homoptera, allied to the Cicadidae, have on the pronotum very strange outgrowths of unknown significance (Figs. 16-21). "It is indeed hard to understand," says Funkhouser (1917, p. 312), "how it is possible for certain forms with wonderfully exaggerated pronotal processes to maintain their balance while flying. It is remarkable that these processes should not be at once broken off in the ordinary activities of the insect. Certainly it is hard to account for such developments by natural selection, and it seems more reasonable to regard the Membracidae as extreme examples of orthogenesis."

FIG. 22.—Gall of *Chermes pectinatae* Chol. on *Picea excelsa*. (From Cholodkovsky, Russian Official Publications. 1915.)

Galls formed by representatives of the genus Chermes on shoots of conifers resemble fir-cones. Especially noteworthy are the galls of *Ch. pectinatae* Chol. on various firs (chiefly on *Abies sibirica*). They consist exclusively of a modified bud and recall an immature cone.[1] In this case the construction of the gall is due to the immediate and direct influence of external excitation (see Figs. 22 and 23). A similar case is mentioned by Darwin ("Variations of Animals and Plants," chap. xxiii, p. 284): Reissek (1843) described a Thesium (fam. Santalaceae), affected by a parasitic fungus (Oecidium), which had become greatly modified and assumed some of the characteristic features of certain allied species, or even genera. "I quote this remark," adds Darwin, "to show how profoundly yet in how natural a

[1] Cholodkovsky, 1895-96; 1912, pp. 458-459, Fig. 394; 1915, Figs. 4, 27.

manner, this plant must have been modified by the parasitic fungus."

We may quote here the opinion (only partially shared by us) of de Vries (Willis, 1922, pp. 226-7) bearing on the same subject of "preadaptation" of characters: "Specific characters have evolved without any relation to their possible significance in the struggle for life. . . . *Everywhere in nature, in geological periods as well as at present*, the morphological characters of newly originated types have no special significance in the struggle for life. . . . They may afterwards prove to be useful or useless,

FIG. 23.—Various forms of galls of *Chermes pectinatae* Chol. on *Picea excelsa*. (From Cholodkovsky, Russian Official Publications, 1915.)

but this has no influence upon their evolution. Obvious instances of usefulness occur, as a rule, only at much later periods during the wandering of the new forms, when unexpectedly they arrive in environments specially fitted for them. The usual phrase, that species are adapted to their environment, *should therefore be read inversely*, stating that most species are now found to live under conditions fit for them. . . . In a popular way we could say that in the long run species choose their best environment. Favourable local conditions induce a rapid multiplication, whereas elsewhere the forms remain rare, or are seen to disappear slowly."

In the present section we have considered *one* of the methods of an orthogenetic formation of characters. Natural selection has played no part in the examples cited. It is characteristic of this method that the origin of characters lies beyond any relation to utility.

We repeat, that in the foregoing we have suggested only one of the methods of the formation of characters.[1] Every now and then characters and responsive actions are purposive or efficient from the beginning.

But there are also certain characters which obviously no organism could effectively utilise. Let us take a few examples. In adult males of *Aphya minuta*, a small fish of the Gobiidae, inhabiting the shores of Europe, teeth are grown which are entirely useless for the animal, as both the males and females perish after the breeding season (Smitt, pp. 266-268). In the Salmonidae, a family which belongs to quite another order of fishes, we can observe the same phenomenon, which is most conspicuous in the Pacific salmon. In the males of the dog salmon (*Oncorhynchus keta*) and humpback salmon (*O. gorbuscha*), when they ascend rivers for spawning, the snout lengthens, large teeth grow in the mouth, and a hump swells out on the back. In the breeding season, and generally while in the rivers, neither the males nor the females of these fishes feed. After the breeding season the males and females all perish. It has been suggested that the large teeth in the breeding males of the Salmonidae are used by them in their fights for the possession of the female; drawings may even be found, in which such fights between males of the European salmon (*Salmo salar*) are very picturesquely displayed. But Soldatov, who has observed the life of the two Pacific salmon just mentioned in the rivers of the Amur basin, denies (p. 107) the sexual character of these fights; males fight against males, but so do females against females. These fights apparently occur in a purely reflex manner, and are caused by the intense nervous excitement to which the fish is subject during the spawning season.

Leptocephalus, the larva of the eel *Anguilla anguilla*, has large, larval teeth, which are shed when the Leptocephalus

[1] To these opinions I have come independently. But similar ideas and suggestions have been developed by Morgan (1903), Cuénot (1914, 1921), and Bateson (1913).

is transformed into the young eel. But these teeth are of no use to the larva, because prior to its metamorphosis it *never* eats.

In the North American Pleistocene mammoth *Elephas columbi*, the tusks were curved so as to be bent inward, and their points crossed each other.[1] Evidently these teeth could have been of no use to their possessors. On the contrary, it seems much more likely that the extinction of the animal was due to such an incongruous organisation. In late Pleistocene time this mammoth yielded its place to another species, *Elephas primigenius*.[2]

All that has been set forth in the present section shows that cases occur in which characters have been formed in a definite direction as a consequence of internal constitutional causes, independently of the degree of utility to the organism, and sometimes to the detriment of the latter.[3]

6. A CONTRIBUTION TO THE HISTORY OF THE QUESTION

Many writers have declared in favour of development following a definite course, or of orthogenesis—Danilevsky (1885), Koken (1893, p. 628; 1902, p. 14), Cope (1896, p. 9), Eimer (1897), W. Scott (1894, pp. 372-373), Heincke (1898, p. civ), Osborn (1907, p. 228),[4] Jaekel (1902), Diener (1910, p. 32), Przibram (iii, 1910, p. 245), Méhely (1912), Steinmann (1911, p. 14), Whitman (1919), Willis (1922, p. 215), and many others.

[1] See Osborn, 1910, p. 155; also Abel, 1912 or 1913, p. 797.

[2] Osborn, *l.c.* p. 441.

[3] Bateson (1913, p. 235) has even expressed the paradoxical opinion that animals exist not thanks to their characters, but in spite of them, and the fact that animals continue to live is but a proof of the balance of their properties weighing somewhat in their favour. With such an opinion, of course, it is impossible to agree.

[4] Osborn uses the term *rectigradation*, which he understands to be the occurrence of new tubercles on the upper and lower teeth in predetermined and definite places, orthogenetically, quite independently in different orders of mammals and at various epochs.

Huxley in his essays ("Mr. Darwin's Critics," 1871; "Darwiniana," p. 181) quite clearly shares the same point of view. Variations, he says, are neither indefinite nor fortuitous, nor does variation take place in all directions. "A whale does not tend to vary in the direction of producing feathers, nor a bird in the direction of developing whale-bone."

If that be the case, if the tendency towards variation be *predetermined*, if the production of variations is governed by law, the importance of natural selection is then reduced to zero, as was admirably expressed by Strakhov so long ago as in 1873: "Every law which is discovered in the phenomena of variation and heredity leads to the refutation of Darwin's theory. The strength of that theory, its intellectual attractiveness, emphatically consists in the supposition that laws do not exist and that phenomena may be reduced to the play of chance." [1]

In view of such argument it is all the more remarkable that this was not evident to Huxley, who thought it possible to unite both principles—that of a definite direction and that of natural selection. In the same essays ("Evolution in Biology," 1878; "Darwiniana," p. 223) he says, "The importance of natural selection will not be impaired even if further inquiries prove that variability is defined, and is determined in certain directions rather than in others, by conditions inherent in that which varies. It is quite conceivable that every species tends to produce varieties of a limited number and kind, and that the effect of natural selection is to favour the development of some of these, while it opposes the development of others along their predetermined lines of modification."

But it must be perfectly evident, that if the formation of new characters is due to the operation of a law, and not to chance, *natural selection loses its position as the guide in* evolution: chance can certainly exterminate any new form,

[1] N. Strakhov, "Darwin," 1873. In his "*Struggle with the Western World*," ii, 1883, pp. 141-142 (in Russian).

but is unable to choose an accidentally useful variation, for utility is produced not by chance, but by law. In this lies the crux of the whole question of evolution: *is the useful produced by chance or by law?*

Metcalf (1913, p. 69) reasons in much the same way as Huxley: the orthogenetic directions which follow the disadvantageous course are subject to annihilation through natural selection. The latter thus exerts an influence upon the course of evolution, and orthogenesis is merely the handmaiden of natural selection (p. 71).

To this the following objection might be made. Of course, all that has become extinct was in some way unfit. Thus, trilobites, ammonites, pterodactyls, dinosaurs and a multitude of forms have become extinct. And, naturally, nothing can be urged against the opinion, that they have been destroyed by means of natural selection (for, of course, their extinction could not have been accomplished by supernatural means). But it is none the less evident that the direction of evolution from this cause can hardly have experienced a considerable change, for a definite direction in the evolution of ammonites and dinosaurs lasted for millions, possibly tens of millions of years, during which ammonites and dinosaurs, in spite of everything, yet managed to exist and to develop. In order that natural selection in the presence of a definite direction in evolution could effectively operate upon development, it would be necessary (1) that a definite direction should last an insignificant period of time, and (2) that there should be an infinite number of such definite directions. But neither of these conditions actually exists.

Plate reasons thus: although individual variations follow different routes, and consequently evolution is possible in many directions, still only a few of the latter lead to progress. These latter are preserved, the remainder perish ("Selektionsprinzip," p. 508). For this process the term "orthoselection" is proposed. This opinion may be opposed by referring to

the case of the evolution of teeth in mammals: variations in that case *do not follow all directions*.

Darwin himself has admitted the importance of development in a determined direction. In the beginning of chap. xxiii of his work on "Variation of Animals and Plants" he says, "By the term definite action, I mean an action of such a nature that, when many individuals of the same variety are exposed during several generations to any particular change in their conditions of life, all, or nearly all, the individuals are modified in the same manner. By such means a new sub-variety may be obtained without the intervention of natural selection." Among other facts Darwin notes (chap. xxiii) that in the hot parts of India an English variety of apple-tree, a Himalayan oak, Prunus and Pyrus all assume a pyramidal habit: "This fact is the more interesting, as a Chinese tropical species of Pyrus naturally grows thus." At Angora not only goats, but shepherd-dogs and cats possess fine fleecy hair. Darwin further refers to the observation of Meehan (1862), who had compared twenty-nine kinds of American trees with their nearest European allies. Both live in the same conditions. In the American trees the leaves are not so deeply toothed or serrate, their buds are smaller; in the autumn the leaves assume before falling a brighter tint; they fall earlier in the season; the seeds are smaller; the trees are more diffuse in growth and have fewer branchlets. Having called attention to these facts Darwin remarks, "Now, considering that these corresponding trees belong to several distinct orders, and that they are adapted to widely different stations, it can hardly be supposed that their differences are of any special service to them in the New and Old Worlds; and if so, such differences cannot have been gained through natural selection, and must be attributed to the long continued action of a different climate."

With reference to similar parallel variations Darwin speaks of a tendency to vary in the same direction.

It is curious to confront this statement with the following words of Darwin in the "Origin of Species" (beginning of chap. v): "I have hitherto sometimes spoken as if variations . . . were due to chance. This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly *our ignorance of the cause of each particular variation.*"

And what if the occurrence of variations should be due to compliance with a certain law? In that case, the value of chance, as well as of natural selection, falls to the ground. This had already been noted by Aristotle in his "Physics" (ii, 198^b 24, Bekker). Adducing the teeth of man as an *example of a purposeful structure*, he says that such *fitness* might be explained by the play of chance: had characters been *accidentally* adapted, then such organisms would be preserved; those, on the contrary, which were bereft of such adaptations would perish. But, adds Aristotle in objection to this argument, what regularly occurs cannot be the effect of chance.[1]

To this it might be objected that the principle of a determined direction in evolution brings us back to the teleological conceptions of Aristotle. We may reply, that according to the doctrine of contemporary physics, all the processes which occur in the inorganic world have a determined direction: or, expressed differently, that the entropy of the *universe tends towards a maximum.* By determining the relation of the quantity of entropy to its maximum quantity at a given moment, we judge of the present from the future. But surely in this consists the essence of teleology. The principles of stability and development contain elements of teleology, says Wundt (ii, p. 66).

From the foregoing it is clear, that our view radically differs from the position of Darwinians, who maintain that variability, upon which natural selection operates, has no determined direction: this variability is so infinite that "at any given moment the very variation that is wanted may

[1] On the importance which the ancients attributed to chance and on their reflections on the struggle for life, see my paper, 1922.

for the most part be found amongst individuals of a commonly occurring species" (Plate, 1913, p. 198). Darwinism, says Plate (p. 222), reckons with variations which occur by chance: it is a theory of accidents (Zufallstheorie). In substantiating this assertion, Plate makes use (p. 199) of an example, which could not have been better chosen for its refutation: "It is conceivable that insects of various groups would assume the outward appearance of ants and leaves, or, molluscs of the most diverse families living on the beach exposed to the surf would acquire a thimble-like shell deprived of convolutions, had they been able to vary in conformity to their history and constitution but in a few directions." But of this we shall treat more fully in the chapter on mimicry.

The discussion we have followed through chapters ii and iii leads us to recognise the following laws:—

I. *Higher characters or their rudiments appear in lower groups very much earlier than they are manifested in full development in organisms occupying a higher position in the system.*

It may be inferred from this that evolution is to a considerable degree an unfolding of pre-existing rudiments. But, as will be seen from the sequel, it would be incorrect to maintain that evolution is preformation pure and simple.

II. *The successive manifestations of new characters are governed by law. In the process of evolution there is no place for chance: new characters appear where they should appear. Evolution is nomogenesis, or development determined by law.*

Just as ontogeny pursues its destined course prescribed by law (the antecedent stage preparing and predetermining the subsequent one), so is evolution accomplished by means of law.

III. Therefore *evolution follows a determined direction.* There is no chaotic variation, as was assumed by Darwin.

IV. *Some characters owe their development to internal (autonomic) causes inherent in the very nature of the organism, and independent of any effects of the environment.* These are the fundamental, the most essential characters which determine the very plan of structure of a given group. It is perfectly obvious that the ontogenetic process, for instance, is effected by these intrinsic causes alone.

V. *The laws of development of the organic world are the same both in ontogeny and phylogeny.* Thereby may be explained the much-talked-of "recapitulation" of phylogeny by ontogeny.

CHAPTER IV

CONVERGENCE

> The coordination of so many animal kinds in a certain general scheme, which apparently underlies the structure not only of the skeleton but of other parts of the body . . . affords our mind however feeble a hope that something might be attained in this matter by the aid of the principle of mechanism of Nature, without which there could exist, speaking generally, no Natural Science. This analogy between forms, in so far as they apparently arise, notwithstanding their manifold differences, in conformity to one general original plan (einem gemeinschaftlichen Urbilde gemäss), strengthens the assumption that they are related to each other through their origin from one common mother by means of a gradual approximation of one kind of animals towards another.
>
> KANT, "Critique of Judgment," 1790, § 80.

FACTS FROM COMPARATIVE ANATOMY

THE adherents of the theory of selection explain *the differences* in the structure of organisms as the result of divergence, *i.e.* of a deviation in different directions of characters, due to variation, accidental utility, struggle for life and the survival of the fittest. *Similarities* are interpreted as being something aboriginal, as a consequence of the inheritance of characters from common ancestors.

But every now and then similar characters are observed in two organisms belonging to two such distinct groups that there can be no question of their having inherited similar characters from common ancestors. Such, for instance, are the similarities between whales and fishes, or dolphins and ichthyosaurs. That in whales and fishes the same characters, and these specially adapted for aquatic life, should have arisen *by chance*, is so incredible that even the followers

of Darwin are loath to adopt this explanation. In such a case the intervention of natural selection is set aside, and it is alleged that similar conditions give rise to similar characters. But one circumstance is lost sight of, namely, that such an interpretation may be adopted only on tacitly recognising the aboriginal fitness of the living being, and this, as we have demonstrated in chapter i, § 1, renders the theory of selection superfluous. However that may be, selectionists are also forced to admit that development *sometimes* follows a determined course: there is no infinite variation, and the character wanted spontaneously occurs, where it should be, without any intervention on the part of the selection of chance variations.

In the following pages will be shown that what in the opinion of adherents of selection is exceptional is really the rule. Convergence of characters *is inconsistent with the principle of chance*; it is a result of development in a determined direction.

In opposition to the commonly accepted view we maintain (and we hope to be able to prove it) (1) that very often differences are not the consequence of divergence of characters, but the effect of inheritance from common ancestors; they are something *aboriginal*; and (2) that very often similarities are not the result of inheritance from common ancestors, but a consequence of *convergence* of characters.

The above does not occur always: *evolution, taken as a* whole, exhibits *differences* both aboriginal and divergent, similarities both aboriginal and convergent. But the general trend of evolution, its primary traits, are due to aboriginal differences and convergent similarities, and this is inconsistent with the theory of natural selection.

True, Darwin was sometimes disposed to explain the phenomena of convergence also by natural selection. Thus, after mentioning the following instances, which presented difficulties for his theory—the occurrence of electrical organs in various groups of fishes, of phosphorescent organs in different

orders of insects, of pollinia (*i.e.* pollen-sacs fused into a coherent mass attached by a stalk to a viscous disc) in such widely separate families as orchids and milk-weeds (Asclepiadaceae). Darwin ("Origin of Species," First Ed., pp. 193-194) adds, "I am inclined to think that as two men have *sometimes independently of one another hit on the same* invention, so . . . it appears that natural selection, working for the good of each being, and taking advantage of analogous variations[1] sometimes modifies nearly in the same way[2] two organs in two living beings, which have inherited but little in common from their common progenitor."

This explanation seems quite improbable. Since every useful variation according to Darwin's theory arises by chance, it is scarcely credible that such a variation should arise accidentally even in one species; but still more incredible would be its occurrence in different species having no common ancestors. Natural selection is powerless to effect anything, if the probability of the occurrence of a certain character may be approximately zero: unless, as it has been tacitly assumed in the passage cited above, the same functions be attributed to natural selection as are attributed to vital force.

1. CONVERGENCE AND HOMOLOGY

Owen (1843) applied the term *analogous* to such organs or parts as possess the same functions in different animals (for instance, the wings of birds and the wings of insects), and *homologous* to identical organs in different animals, however diverse may be their shape and functions; thus, for instance, the wings of birds and the anterior extremities of whales are homologous organs. Analogy is a superficial resemblance, homology a resemblance based on a common origin. The first is founded on physiology, the second on

[1] In the sixth edition (p. 152), "all favourable variations."

[2] In the sixth edition, "has produced similar organs, as far as function is concerned."

morphology. Such is the commonly accepted distinction between these two terms.

But similarity may be exhibited in phenomena which hold, as it were, an intermediate position between the above-given definitions. It happens not infrequently that homologous organs "under the effect of similar conditions" (the customary phrase in such cases) develop similar characters. To such a case we have referred earlier (chap. i) in speaking of a determined direction in the development of teeth in mammals. Analogies may further be encountered both in related and in unrelated forms. Conformably with this, Osborn (1902, p. 261)[1] submits the following classifications of analogous variations:

1. *Parallelism*: an independent (not due to inheritance from common ancestors) acquisition by related animals of similar characters.

2. *Convergence*: an independent acquisition by unrelated animals of similar characters.

3. "*Homoplasy*"[2] (potential, or latent homology, isomorphy): an independent acquisition of similarity between homologous organs in different animals (cf. above, example of teeth).

4. *Analogous variation*: "similar congenital variation in more or less distantly related animals and plants."

In the present chapter we shall make no difference between parallelism and convergence, and shall employ the term "convergence" to denote both phenomena, as the conceptions "related" and "unrelated" may be substituted one for the other according to the point of view. More interest is attached to the phenomenon designated by Osborn "homoplasy"; to it we shall apply the term "isomorphy" proposed by Fürbringer.[3] Isomorphy is

[1] See also Osborn, "Science," xxi, 1905, pp. 959-961.

[2] The term "homoplasy," proposed in 1870 by Ray Lankester, is synonymous with convergence, as has been explained by its author in a letter to Osborn; see Osborn, 1907, pp. 228, 238.

[3] "Convergenz-Analogie oder Isomorphie," Fürbringer, 1888, pp. 1478-9.

something intermediate between convergence and homology. Everything that will be presented henceforth in this chapter will show that between convergence and homology there is no difference in principle : all characters arise in accordance

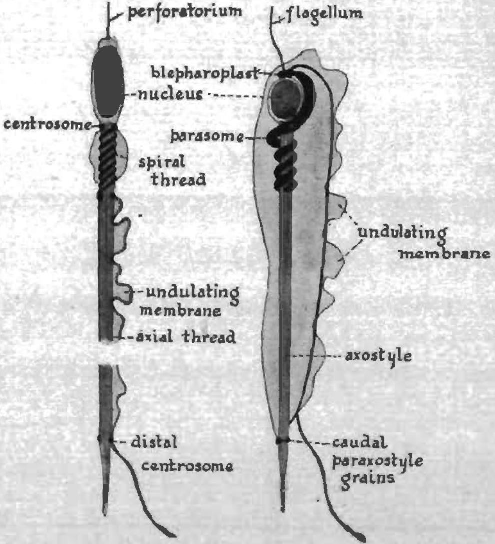

FIG. 24.—Spermatozoon (to the left) and flagellate (Trichomonas, to the right). Diagrams.
(After Alexeieff, Russian Official Publications.)

with certain laws. The resemblance between organisms in certain characters *may* be due to consanguinity (blood relationship), but *may* be the result of development subject to the same laws : resemblances may be either homologous or convergent. Similarity in the organisation of two forms

need not oblige us to admit their common origin ; it merely shows a certain uniformity in the laws of nature. The forms of the weathering of rocks in deserts throughout the entire world are alike, but that does not compel us to infer that similar forms, say, of mountains, are derived from one common form.

Darwin believed that blood relationship or "community of descent" is "the one known cause of close similarity in organic beings."[1] We shall subsequently offer many instances showing that far-reaching similarities may be acquired by forms possessing no reciprocal blood relationship. Here we may confine ourselves to one example, *i.e.* the resemblance long ago detected in the structure of spermatozoa and of parasitic flagellates.

A. Alexeieff (1923), for instance, draws attention to the fact that the spermatozoon of a European toad *Bombinator igneus* is very like the flagellate *Trichomonas angusta* Alex. This resemblance may be followed out more fully in detail (Fig. 24) :

Spermatozoon (diagram).	*Flagellate* (Trichomonas, but the parasome from Devescovina).
Perforatorium - - -	Anterior flagella + corresponding part of the blepharoplast
"Coiffe céphalique" - -	Calyx
Head - - - - -	Nucleus
Proximal centrosome + upper part of the distal centrosome	Dorsal part of the blepharoplast
Spiral thread - - -	Parasome
Axial filament - - -	Axostyle
Lower half of the distal centrosome	Caudal paraxostyle grains
End part - - - -	End spine of the axostyle
Undulating membrane (+costa)	Undulating membrane (+costa)
Caudal "manchette" (rest of plasma) - - - -	Plasmatic body

[1] "Origin of Species," 6th ed., chap. xiv, p. 365.

The axial filament of the spermatozoon is formed from the centrosome; the axostyle of the flagellates, according to the researches of Alexeieff, is produced from the blepharoplast, which is a homologue of the centrosome.

The resemblance between the spermatozoon and the flagellate is striking, and is carried out in the minutest details. This resemblance is regarded by Alexeieff as convergence due to the same surrounding conditions: trichomonads are parasites inhabiting the mucus of various organs (*e.g.* of man), spermatozoa are adapted to live in the viscous medium of the seminal fluid.

In any case, we are generally unable to tell whether we have to do with homology or analogy. For all we know in the matter refers solely to resemblances and differences. *In establishing the origin of organisms our judgment is based on such resemblances and diversities, and not vice versa*: we can never deduce resemblances between organisms from their origin, the derivation of forms from other forms having never been witnessed (beyond minute forms which have no evolutionary value). That Amphibia are derived from fishes has been *inferred* from the *similarities* subsisting between primitive Amphibia (Stegocephala) and crossopterygian fishes. There are no other grounds for deriving the former from the latter. Therefore Rauther (1912, p. 122) is perfectly right in observing that Gegenbaur falls into a vicious circle by advising us to study the genealogical relations of organisms for the proper discrimination of homologies and analogies. Our appreciation of genealogical relations is based on these very similarities of which we are unable to say whether they are homologous or analogous.

Spemann (1916, pp. 78-79, 82) asks whether the crystalline lens of a tailed amphibian normally formed from the ectoderm of the embryo at the spot where the optic vesicle adjoins the side of the head is homologous with a lens artificially regenerated after its removal; for in the case of regeneration the lens in the newt is formed, not from the

cornea, as might be supposed, but from the upper margin of the iris, *i.e.* from quite a different substance, yet the resultant product is histologically perfectly identical with the normal lens. Nor is that all. If in the embryo of the frog the ectoderm from above the primitive optic vesicle be removed, and a piece of skin be transplanted from another part of the body on to that very spot, a lens will still be formed from that skin. Is the latter homologous with the normal lens? In certain vertebrates it is possible in the earlier phases of development, while the optic vesicles have not yet differentiated, to cut the embryo in two, when a complete individual will be regenerated from each half. In that case, asks Spemann, would the eyes of these two individuals be homologous with the eyes of a single normal individual?

It has sometimes been stated (Abel, 1912, p. 618) that convergence (and parallelism) only leads to an external similarity. Further on we shall show that, on the contrary, convergence affects organs that are the most essential from the standpoint of comparative anatomy.

If, guided by facts from palaeontology, we trace the evolution of several groups of animals and plants, belonging to different divisions, we shall be obliged to admit that the course of evolution was as follows: a given group of organisms in the course of time breaks up into forms which either repeat the course of development of the existing forms, or follow a direction in which will subsequently develop still more highly organised groups. Nature refuses, as it were, to utilise the diversity of means at her disposal for the production of new forms, and takes advantage of only a restricted number of *definite* possibilities. She admits variety in details, while endeavouring to preserve a certain number of fundamental types, at the same time mingling together characters of different types in one group; and this circumstance causes us to detect similarities in several directions at once. But this clearly testifies in favour of convergence. Let us take some examples. In the lower Palaeozoic and

Mesozoic reptiles we may observe several phylogenetic routes leading in the direction of birds and mammals (of different orders of these classes), but actually giving origin to neither. The Selachii clearly exhibit in various groups characters of development leading in the direction of terrestrial vertebrates: but the Tetrapoda have never been derived from the Selachii.

The Palaeozoic club-mosses obviously develop in the direction of the higher gymnosperms. Bennettitales, Mesozoic gymnosperms, in their development follow in the direction of flowering plants (see chap. ii, § 2), although they are not the ancestors of these. The same phenomena may be observed in the organisms now living. Monocotyledons copy the dicotyledons in many ways. In § 6 of this chapter it will be shown that invertebrates of the most different groups acquire vertebrate characters. The Marsupialia consist of several groups, which are analogous with those of the Placentalia. The phenomenon in question may be traced with exceptional clearness in the insects, the mutual blood relationships of which have recently been investigated with especial care.

2. INSECTS

The class of insects falls into a number of orders, over thirty, every one of which exhibits similarities with a series of other orders, sometimes very widely separated. Since these orders are so numerous and the similarities referred to relate to the most diverse organs, both internal and external, it is evident that these similarities cannot be the effect of inheritance from one common ancestor, for this imaginary ancestor would have to possess all the "perfections" at once, the characters of the butterfly, of the fly, and of the bug. It is obvious that in the case of insects we have to deal with a manifestation of convergence, which, we repeat, *affects all the organs*.

Let us begin by examining the relationship of a motley group of insects, which are sometimes united together under the designation of Neuroptera (Pseudoneuroptera and Neuroptera proper). This union is, we repeat, artificial, but, in any case, all the representatives of the group possess a complex of similar characters. Namely, in the imago the mouth parts are of the masticating type; of wings, if present, there are two pairs, all membranous; the venation of the wings is usually highly developed, the longitudinal veins forming with the transverse ones a close network of cells.

Among the Pseudoneuroptera, the Mallophaga display a resemblance on the one hand with the Psocidae, on the other with lice (Pediculidae), these latter being allied to bugs (Hemiptera).[1] The resemblance of the Mallophaga with lice is not confined to their outward appearance or manner of life, but extends to the structure of the intestine, genital organs, nervous system, and even to the embryonic development (Cholodkovsky, 1912, i, p. 408). But the mandibles of the Mallophaga are not of the suctorial type, as in the lice, but are masticatory, as in the Neuroptera proper.

The Embioidei (a small group of insects distributed, among other places, both in Southern Europe and the Crimea) exhibit a similarity with the Orthoptera; in particular, as is indicated by N. J. Kuznetsov, they are very like the singular Australian cricket Cylindrodes. Embryological features show similarity with the Orthoptera and termites.

> In certain very fundamental respects termites resemble the Blattoidei (some even find rudiments of social life in cockroaches); in others they resemble the Psocidae. The Blattoidei flourished in Upper Carboniferous and Permian times, whereas termites are only known since the Lower Tertiary (Handlirsch, p. 1240); but I am informed

[1] On the relationship of various groups of insects see a detailed article by Crampton, 1919, where a copious list of authorities is given. See also Handlirsch, 1906-08, p. 1227 *sq.*, and Sharp-Kuznetsov.

by A. V. Martynov, that, in his opinion, there are grounds for assuming that they will be discovered in the Palaeozoic strata, as this group of insects is a very ancient one, parallel to the cockroaches.

The Psocidae show a likeness to beetles (a fossil psocid, Sphaeropsocus, from amber possesses "elytra" which unite on the back with a median suture as in beetles),[1] earwigs (Dermaptera), Embioidei, termites, Mallophaga, and stone-flies (Crampton, pp. 101-102). In *Amphientomon paradoxum* the body and its appendages are covered with scales, as in butterflies.

Dragon-flies are very like certain true Neuroptera, such as Stilbopteryx (belonging to a family allied to the ant-lions) not only in external appearance, but in habits.

The Mecoptera (Panorpatae), or scorpion-flies, display a resemblance to Diptera (*Bittacus tipularius* is very like the daddy-long-legs, Tipula), to Hymenoptera (the genital organs of the males of Mecoptera resemble those of the saw-flies ; the larvae of the latter are like the larvae of scorpion-flies, (Crampton, pp. 106-107)), and to true Neuroptera, such as Nemoptera and Nymphes. The larvae of Mecoptera resemble the caterpillars of primitive Lepidoptera of the Eriocephalidae (Handlirsch, p. 1254).

The Neuroptera genuina bear a resemblance to may-flies, dragon-flies and termites ; the larvae of some forms are very like those of beetles.

Caddis-flies (Trichoptera) exhibit many common structural features with the true Neuroptera, Mecoptera and, lastly, with Lepidoptera (Trichoptera and Mecoptera are known since the Lias, Lepidoptera since the Middle Jurassic). The resemblance of the Lepidoptera of the genus Micropteryx to the Trichoptera is so great that Comstock (1918) separated the Micropterygidae from the Lepidoptera and joined them to the Trichoptera (Chapman, quite recently, has promoted the Micropterygidae to the rank of a special order Zeugloptera, which is thus separated from the Lepidoptera).[2]

Thus the various groups of the lowly organised insects of the heterogeneous assemblage "Neuroptera" display

[1] G. G. Jacobson has drawn my attention to the fact that the fauna of the Petersburg Government includes a fly, Stegana, in which the wings are folded in the same manner.

[2] Crampton, 1919, p. 113.

similarities with higher groups, *i.e.* Diptera, Hemiptera, Lepidoptera and Hymenoptera. Such a circumstance clearly testifies in favour of convergence.

Many other instances might be given. Among insects we meet everywhere with a convergent development, *i.e.* one having a definite direction; and this is equivalent to the absence of infinite variations from which accidentally useful ones might be selected.

3. CONVERGENCE OF INVERTEBRATES AND VERTEBRATES

Among invertebrates several groups may be named which exhibit a certain resemblance with vertebrates, sometimes in the most fundamental characters. To such groups may be referred (1) the Tunicata, (2) Enteropneusta (*Balanoglossus* and others), (3) Annelida, and (4) Nemertinea. There are adherents of the origin of vertebrates from every one of these groups. Those (Haeckel, Bateson, 1886; Schimkewitsch, 1889, 1918), who derive vertebrates, say, from Balanoglossus (or allied forms), are inclined to attribute their reciprocal similarities to blood relationship, but in the points of likeness between vertebrates and annelids see a manifestation of convergence. In a corresponding manner are modified the views of those who derive the vertebrates from the annelids (Semper, 1875-6; Dohrn, 1875, 1881-2; Delsman, 1912, from the trochophore).

Wherever lies the truth, one thing is certain, that the similarity of vertebrates to some one of the groups mentioned is due to convergence. If it be true that vertebrates owe their origin to Balanoglossus-like forms, to convergence then may be attributed the following fundamental characters of vertebrates, which ally them to the annelids: conspicuous metamery, a resemblance in the structure of the urinogenital system (especially noteworthy is this likeness, discovered by Boveri and Goodrich, in the structure of the excretory organs in annelids and Amphioxus), the circulatory

system, the olfactory organs and those of the lateral line.[1] If, on the other hand, vertebrates be derived from annelids, as is assumed by Semper (1875-76), Dohrn (1875, 1881-2), Delsman (1913), convergence would then be credited with the presence in the vertebrates of the following characters common also to the Enteropneusta—gill-slits, dorsal neural tube, notochord. If the Enteropneusta, annelids and vertebrates rise from one common stock, this would signify that all their reciprocal similarities were due to convergence, for, of course, it would be impossible to admit that the common ancestor had concentrated in itself all those features of high specialisation, which have induced us to draw the Annelida, Enteropneusta and vertebrates close to one another. If, finally, it be admitted that vertebrates had a polyphyletic origin, *i.e.* that they have been derived from different groups (the most probable assumption), in that case also a series of fundamental organs would then have been produced by convergence.

Not infrequently Dohrn's view is followed, *i.e.* that the Tunicata are regressive forms derived from vertebrates; it is alleged that in some of the Tunicata regression is accompanied by a sessile habit. By means of regression the absence in the Tunicata of metamery, of the secondary body cavity and of nephridia may be accounted for. But how to explain, asks Delsman (p. 705), the presence in the larvae of ascidians of the statocyst (otocyst) and of the eye-like organ? Can it be possible that these organs were reduced at first, and then appeared again?

It is much more likely that the character in which the adult Tunicata bear resemblance to the vertebrates, namely, the presence of gill-slits, is due to convergence, while the occurrence in the larva of the notochord and of the dorsal nervous tube is the manifestation of phylogenetic acceleration.

[1] For details, see Delsman, 1913, p. 704. The organs of the lateral line in annelid worms have been thoroughly investigated by Eisig (1887); see Delsman (pp. 686-7) on the subject.

We may here refer to the detailed investigations of Zawarzin (1923) on the histological structure of the nervous system in vertebrates and invertebrates. The structure of the optic centres in Daphnia, insects, Cephalopoda and vertebrates is in principle the same. The structure of the ventral chain in the larva of the dragon-fly or of the ventral nerve-cord of the earth-worm corresponds in detail with that of the spinal cord of Ammocoetes. By what can such resemblances be accounted for if not by convergence? The common roots of Crustacea, Insecta, Mollusca and Chordata, if we agree with Schimkewitsch (1918, p. 311), ascend to the Coelenterata. The supposition that Coelenterata had already possessed the nervous system of the type in question may be set aside as being simply absurd.

From the examples set forth in this section, it is obvious that convergence affects the most important organs, fundamental for existence, and not merely external characters, as is assumed by Abel.

4. AMPHIOXUS, LAMPREYS, FISHES

1. However close at first sight may be the resemblance in the structure of Amphioxus to that of other vertebrates, *i.e.* Craniata, after a careful examination such cardinal differences between the two become manifest that it is impossible to derive the Craniata from the Acrania. And, indeed, in the peribranchial cavity, the branchial apparatus, the urino-genital system and the histological structure of the tissues, Amphioxus and the Craniata radically differ. Therefore, it must be admitted with Vialleton (1911, p. 592) that the similarities between the Craniata and Acrania are due to convergence, originating in the first place in the presence of a segmented muscular system.

Delsman (1913, pp. 704-705), the most recent of writers on the origin of vertebrates (or, to be more exact, of the Craniata), considers the annelids, as has been noted above,

to be their ancestors.[1] As regards Amphioxus and the ascidians, Delsman maintains that it is impossible to derive them conjointly with the Craniata from one common stock. Neither can the Craniata be derived from the Acrania, nor can the Acrania be regarded as degraded Craniata (p. 704). Delsman, as well as Vialleton, comes to the conclusion that similarities in the structure of ascidians, Amphioxus and the Craniata are due to convergence; in opposition to Dohrn, who regarded Amphioxus as a degenerate marsipobranch.

2. Just a few words about the Marsipobranchii (lampreys and hags). They are also derived by Dohrn from the Gnathostomata (vertebrates possessing jaws), in which the jaws were reduced owing to "parasitism," and transformed into a suctorial apparatus. Other writers, such as Huxley and Parker, regarded lampreys as primitive fish. Lastly, from Haeckel (1866; 1895, pp. 216, 222) is derived the opinion that lampreys are a peculiar lateral branch. A. N. Séwertzov (1917) rejects Dohrn's hypothesis, assuming that both the lampreys and the Gnathostomata possessed common ancestors. In the meantime, it must be acknowledged that, in both, certain characters have arisen by means of convergence, as, for instance, the dorsal commissures between the visceral arches (p. 469), the differentiation of the muscles of the eye, especially of those that are innervated by the oculomotor and the abducens (p. 477), the secondary segmentation of the sub-branchial musculature of the body in the lamprey and its subdivision into separate muscles in the fishes (p. 485-6), branchial filaments (p. 541), etc. At the same time it is alleged that the common ancestor of the Marsipobranchii and Gnathostomata, the so-called Protocraniate, was endowed with a series of characters of high specialisation, such as the brain, eyes, auditory organs, etc.

3. In the Dipnoi and amphibians parallelism is displayed

[1] I think it necessary to point out that I entirely disagree with Delsman in his theory of the origin of vertebrates, as I consider it to be highly artificial.

in the most fundamental features of the organism. Formerly, when it was assumed with Haeckel (1866, 1895, p. 266) and Darwin [1] that the ancestors of amphibians had been derived from dipnoan fishes, the similarity in the organisation of the two groups did not seem remarkable. But now since the researches of Boas, Pollard (1891), Cope (1896, p. 91), Kingsley (1892), Dollo (1895, p. 111), Baur (1896) and Suschkin (1910), we know there can be no question of the origin of amphibians from the Dipnoi. According to the view now generally accepted, the tetrapodous vertebrates owe their origin to forms allied to the Crossopterygii [2] (of which Polypterus is a representative), as, for instance, from forms similar to Eusthenopteron, a fish of the family of Rhizodontidae, from the Upper Devonian of Canada.

The skeletal elements supporting the ventral fins of Eusthenopteron present a wonderful likeness to what we observe in tetrapodous vertebrates.[3] The dermal bones of the skull of Crossopterygii display a remarkable similarity to that of the skull of the Stegocephala, the most ancient tetrapods. In the skull of the Stegocephala we find the following bones corresponding to those of the Crossopterygii: premaxillary, maxillary, nasal, frontal, prefrontal, squamosal (pterotic), postfrontal. The quadratojugal of the Stegocephala corresponds to the sub-operculum (Moodie, 1915, p. 639). In Polypterus, the structure of which is better known, we find the following

[1] See "Descent of Man," 1871, chap. iv.

[2] By the term Crossopterygii is usually designated (as, for instance, by S. Woodward, 1891), after Huxley (1861), a group of fishes having lobed paired fins and bony plates placed between the rami of the mandible, and supplanting the branchiostegal rays. Woodward subdivides them into sub-orders: Haplistia (genus Tarrasius), Rhipidistia (Holoptychiidae, Osteolepidae and others), Actinistia (Coelacanthidae) and Cladistia (Polypteridae). But Goodrich (1909, pp. 278-279, 290, table on pp. 228-229) justly regards the group of Crossopterygii, comprised within such wide limits, as heterogeneous, and therefore divides it into three sections, each of which is equivalent to Actinopterygii, namely: (1) Osteolepidoti (= Haplistia + Rhipidistia), (2) Coelacanthini and (3) Polypterini. The so-called Crossopterygii are thus constituted of three parallel branches, in their turn developing convergently.

[3] See Goodrich, 1901; also Schmalhausen, 1915, p. 22; Suschkin, 1910, p. 250.

features of the higher (terrestrial) vertebrates (Tetrapoda). A two-lobed air-bladder lies on the ventral side and opens ventrally into the oesophagus: its aperture is supplied with muscles and may open and close, so that it is even permissible to speak of a rudimentary larynx. The air-bladder in Polypterus is, on the whole, in a transitional state towards becoming transformed into lungs, and in connection with this an incipient transformation of the circulatory system into the type of one requisite for pulmonary respiration is observed; the occurrence of something like the posterior vena cava may be noted. Polypterus, further, besides the lower, possesses upper ribs, a vomer, paired as in amphibians, and the symplectic is absent.

All the above affords grounds for deriving the tetrapodous vertebrates rather from the Crossopterygii.[1]

Thus, the dipnoan fishes and terrestrial vertebrates present, as it were, two parallel stems. And yet we see in Dipnoi a series of organs and characters which may be paralleled with those of the amphibians and are quite independently developed.

Such are:—

1. The lungs, which are paired in *Protopterus* and *Lepidosiren*.

2. A partition of the auricle into right and left halves is indicated; the pulmonary vein, conveying arterial blood to the heart, opens into the left part of the sinus venosus and supplies the heart with blood through the left half of the auricle; the venous blood, on the contrary, flows into the ventricle by way of the right part of the sinus venosus and into the right half of the auricle.

[1] Still, one cannot be too cautious here, as possibly these similarities are also due to convergence. It is remarkable that the most ancient Crossopterygians (Osteolepis, Eusthenopteron and others) are known from the Devonian. To the same period belong the impressions of a fairly large tetrapod, 60-70 cm. long, described by March (1896) from the Upper Devonian of Pennsylvania, under the name of *Thinopus antiquus*. Thus the tetrapods are contemporary with the Crossopterygii, and this alone should induce us to be careful in sharing opinions which tend to derive Tetrapoda from Crossopterygii. Some Lower Carboniferous Stegocephala are already so highly differentiated that there can be no thought of their direct origin from fishes.

3. The ventricle is prolonged into a spirally curved conus arteriosus, which is provided internally with a longitudinal spiral septum, consisting of a series of valves.

4. The circulatory system, on the whole, begins to show *modifications adapting it to pulmonary respiration*.

5. In connection with this, the nasal apertures open into the mouth cavity.

6. The skull is autostylic, *i.e.* the palatoquadrate is fused with the cranium, the hyomandibular being excluded from the suspensorium.[1]

7. The skull has a large squamosal (pterotic), much resembling the squamosal of Amphibia.

8. In distinction from fishes and in correspondence with what occurs in terrestrial vertebrates, in the temporal region is formed a covering of dermal bones, which is connected with the skull only in the anterior region. In terrestrial vertebrates this covering is subject to diverse modifications and sometimes to reduction, but in any case its remnants may still be observed in mammals in the zygomatic arch (see J. Boas, 1915, on the subject).

9. The pelvis very much resembles that of the lower Amphibia.

10. A posterior vena cava, as in Tetrapoda (a homologue occurs in Polypterus), is present.

11. As in the Amphibia, the hepatic veins in Protopterus open into the posterior vena cava.

12. The hemispheres of the brain are well developed, the pallium is fairly thick, and the cerebellum, as in amphibians, is reduced.

13. In the fore-brain, for the first time in fishes, appears the hippocampus, which occurs in the limbless amphibians (Gymnophiona), in all birds and mammals.[2]

14. A cloaca is present, and a similarity in the urinogenital system may be observed.

And yet, besides these features of higher organisation, we find in the Dipnoi a series of characters denoting their very lowly structure: the notochord is persistent, there being no vertebral centra, the skeleton of the paired fins is cartilaginous, there is a considerable quantity of

[1] On autostylism having convergently arisen in Dipnoi and Tetrapoda, see Schmalhausen, 1923.

[2] On the hippocampus in reptiles see above, chap. ii.

> cartilage in the skull, the maxillary and premaxillary are absent, and the membrane bones of the lower jaw are only indicated, etc. The above leads us to regard the Dipnoi as a group of fishes which, by means of phylogenetic acceleration, have acquired a series of characters of the Tetrapoda.

So far as may be judged, the ancestors of the Dipnoi and those of the Crossopterygii originate not far from one another; somewhere from the vicinity may have diverged the ancestors of the Tetrapoda. It is now generally believed that the Dipnoi are derived directly from the Crossopterygii; but such can hardly be the case.

It seems incredible that in the Dipnoi and in the ancestors of the Amphibia chance characters arose, which enabled both to transform a branchial into a pulmonary respiration: such a transformation would require a simultaneous modification not of one, but of a number of systems, including the heart, the vessels, the nasal cavity, the lungs, the muscles, etc. That all this should have been combined into one harmonious whole by means of accidental variations of characters, and that such a consummation should have been effected simultaneously in the two groups, the Dipnoi and the ancestors of the Amphibia, is a miracle which no naturalist ought to credit. The theory of thermodynamics, based on statistics, demonstrates that "anything may happen," provided sufficient time is allowed for the purpose. Thus a stone may rise "by itself" to a height of several metres: but the theory of probabilities shows that such an event might happen once in the course of such a number of years, which would have to be expressed in the quantity 10 raised to the power of ten thousand millions. Such a probability in the world we live in practically amounts to impossibility. But the probability of an *accidental* occurrence in two different groups of a combination of characters leading from aquatic to atmospheric breathing is still less.

The potential ability to breathe with lungs was evidently

possessed by the Crossopterygii, and by the ancestors both of the Dipnoi and the terrestrial vertebrates.

The parallelism between the Dipnoi and the Amphibia shows that organisms develop conformably to their inner and inherent forces, which, in the presence of certain conditions, succeed in being embodied in definite forms.

This single example of parallelism offered by us is sufficient to reveal the entire inadequacy of the theory of the selection of chance variations.

It is remarkable that adaptation to atmospheric respiration developed, quite independently of Polypterus and the Dipnoi, in certain Teleostei, such as Anabas[1] and Monopterus. In all these cases, in connection with such a transformation, modifications in the circulatory system may be observed, which result in arterial blood, besides venous, being conveyed to the heart.

5 DINOSAURIA

Similarities between dinosaurs and birds. Dinosaurs, fossil Mesozoic reptiles, at one time occupied the place on land now held by mammals. They were distributed in time from the Triassic to the end of the Upper Cretaceous (possibly even to the Palaeocene of North America and Patagonia). They numbered amongst them herbivorous forms (Sauropoda) and carnivorous (such as Theropoda), quadrupedal and bipedal or bird-like forms. The group of dinosaurs is polyphyletic, falling into two distinct orders, which have evidently originated independently (Seeley; Huene, 1914, p. 41);[2] these are the Saurischia with the pelvis of a crocodile, and the Ornithischia with that of a bird. The difference in the pelvis is the more remarkable,

[1] Henninger, p. 270.

[2] Huene (1907-8, p. 404) formerly regarded the dinosaurs as being monophyletic, and derived the Ornithischia from the Saurischia. Abel (1919, p. 576) also acknowledges the diphyletic origin of dinosaurs, separating them into two orders, Dinosauria (= Saurischia) and Ornithischia.

if account be taken of the fact that the majority both of the Saurischia and of the Ornithischia were, like birds, bipedal. Matthew further subdivides these orders into the following sub-orders (1915, p. 32):

1. Saurischia: Coelurosauria (Compsognatha), Pachypodosauria, Theropoda, Sauropoda.

2. Ornithischia (=Orthopoda=Praedentata): Ornithopoda (=Iguanodontia), Stegosauria, Ceratopsia.

It is remarkable that in their structure the dinosaurs exhibit some of the most typical characters of birds.

> In many the bones were pneumatic, although none of the saurians could fly; in the Ornithischia, dinosaurs with the pelvis of a bird, there is not the slightest indication in the structure of their fore-limbs of any incipient transformation of those members into wings. In the Coelurosauria (as, for instance, in Compsognathus and Coelurus), which progressed by leaping on their hind-limbs, not only the bones of the extremities, but even the vertebrae possessed internal cavities. In the Theropoda the bones of the extremities (sometimes of the vertebrae) were hollow. In the Sauropoda the bones of the extremities were nearly solid, but the (trunk) vertebrae possessed cavities, sometimes very extensive (for instance, in Pelorosaurus).[1] Cavities in the extremities and in the vertebrae were present likewise in some of the Ornithischia. Into the dinosaurs' cavities there evidently penetrated, as in birds, the air-sacs of the lungs. This circumstance afforded Haeckel (1895, p. 371) the ground for assuming that the dinosaurs possessed a four-chambered heart (as in birds) and were warm-blooded; Fürbringer (1900, pp. 656-7) and Gadow (1901, p. 415) consider that to be likely.[2]

[1] It is remarkable that, in distinction from birds, it was the smallest dinosaurs which possessed the highest development of pneumaticity in the bones. Such were Compsognathus, half a metre long, Coelurus, of the size of a Varanus lizard, and Hallopus, of the size of a rabbit. In the meantime, such giants as Stegosaurus and Triceratops had solid bones. It would therefore be wrong to regard the pneumaticity of the bones in dinosaurs as an adaptation to a reduction in the weight of the skeleton (Fürbringer, 1900, pp. 657-658). We may here note that in Archaeopteryx the skeleton was not pneumatic.

[2] Fürbringer (1900, p. 659), however, reports certain facts which seem

But the dinosaurs have other characters common to birds; in the Ornithopoda, in connection with a definite

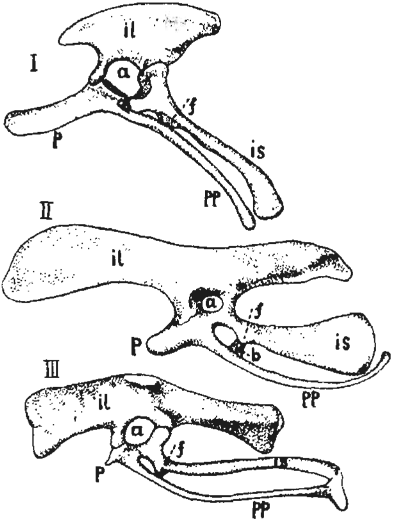

FIG. 25.—Pelvis of dinosaurs and birds. (Left side.) I. Camptosaurus, a dinosaur belonging to the Ornithiscida; II. Young Crypturus, a bird; III. American ostrich, Rhea.

a. acetabulum; *b*. ligament; *f*. process of the ischium; *il*. ilium; *is*. ischium; *p*. pubis; *pp*. post-pubis.

(From J. Boas, "Die Kultur der Gegenwart. Abstammungslehre." B. G. Teubner Leipzig and Berlin.)

tendency to walk on their *hind-limbs*, a long and thin process (post-pubis) of the pubic bone projects downwards and backwards, parallel to the ischium, whereby

to be antagonistic to the theory of the dinosaurs being warm-blooded. Haeckel (1895, pp. 7, 370), departing from the assumption that the dinosaurs and pterodactyls were warm-blooded, separates them into a distinct class, the Dracones.

the pubic region in Iguanodon, for instance, becomes very like what we observe in birds (in which the pubis is bent backward and is parallel to the ischium).[1] The pubic symphysis is absent, as in the overwhelming majority of birds. (See Fig. 25.)

Existing reptiles, as a rule, have two (rarely three) sacral vertebrae, recent birds 9 to 25 (Fürbringer, 1888, p. 1599), but Archaeopteryx only 5 or 6. In the dinosaurs the number of sacral vertebrae, in comparison to the reptiles now living, is increased, being from 3 to 10 (in Saurischia 3 to 5); at the same time a tendency towards a gradual increase in their number is observed: thus, in the Triassic and Jurassic forms there are often 3, and in the Upper Cretaceous Triceratops as many as 10.

In certain dinosaurs (Compsognathus, Ornithomimus and others) the astragalus is closely attached to the lower end of the tibia, just as in the young ostrich (in adult birds the astragalus coalesces with the tibia). In shape the astragalus in Ornithomimus (fam. Compsognathidae of the Saurischia, from the Upper Cretaceous of North America) very much resembles that of the young ostrich. In Compsognathus the distal tarsalia begin to fuse with the metatarsalia, as if to form the tarso-metatarsus, so characteristic a structure in the bird's hind-limbs. In birds, in the formation of the tarso-metatarsus, the second, third and fourth metatarsalia bring in their share, the first remaining independent (not infrequently reduced), while the fifth is totally absent; in this combination the upper end of the third metatarsal lies behind the second and the fourth. Conformably, the tarso-metatarsus of Ornithomimus consists of three metatarsalia, the second, third and fourth, while the position of the upper end of the third strikingly resembles what occurs in birds. (See Fig. 26.)

[1] In Mehnert's opinion (1888) the post-pubis of Ornithischia, although remarkably like the pubis of birds, is not its homologue (see Fürbringer on the subject, 1888, pp. 1045-6, 1609-10). Huene maintains a different view (1907-8, p. 358; 1914, p. 40): the post-pubis of the Ornithischia is homologous with the pubis of birds, lizards and tortoises; birds have passed a stage, when, as the Ornithischia, they had a pre-pubis; in the embryo of *Casuarius galeatus*, according to Sabatier (1880), a remnant of the pre-pubis may be observed. J. Boas (1914, p. 568, Figs. 19-21) also declares in favour of a homology subsisting between the pubis of birds and the post-pubis of Ornithischia.

The first digit in the foot of many dinosaurs (Hypsilophodon among the Orthopoda, Allosaurus and Tyrannosaurus among the Theropoda, and others) is contraposed

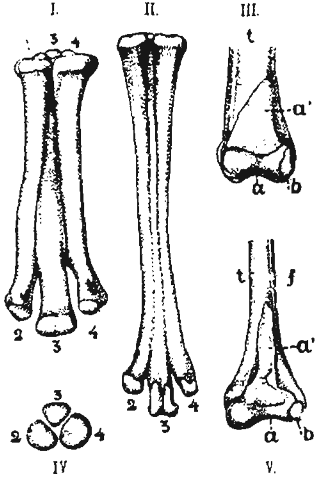

FIG. 26.—I. Tarso-metatarsus of Ornithomimus, a dinosaur belonging to the Saurischia. II. Same in a young turkey. III. Same seen from above. IV. Lower end of tibia and proximal part of tarsus in Ornithomimus. V. Same in a young ostrich.

a and *b*, two bones of the tarsus; *a'*, process of the bone *a*; *f*, fibula; *t*, tibia; 2, 3, 4, metatarsalia.

(From J. Boas, "Die Kultur der Gegenwart. Abstammungslehre." B. G. Teubner, Leipzig and Berlin, 1914.)

and reversed, as in birds (Abel, pp. 156-162), and that of some is rudimentary (as in Ornithomimus, Iguanodon, Stegosaurus) or completely disappears (Triceratops); this condition likewise occurs in birds (thus the first is wanting in the ostrich, the rhea, cassowary, great bustard, plovers (Charadrius), auk, etc.).

The scapula and the coracoid, as in keel-less birds, often coalesce.

In many forms the femur is shorter than the tibia. According to the researches of Dollo (1883) the femur in Iguanodon is constructed on the exact model of the corresponding bone in birds (see also Osborn, 1900, p. 784).

In the Sauropoda the spinous processes of the cervical vertebrae are not infrequently rudimentary or deficient, and of the anterior thoracic vertebrae, bipartite. Osborn (1900, pp. 786-787) points to the resemblance of the cervical and anterior thoracic vertebrae in the dinosaurs Camarosaurus (of the Sauropoda) to what occurs in the emu (Dromaeus). In Diplodocus the vertebral column also displays a resemblance to that of birds.

Further features of an ornithic structure in dinosaurs are the presence between the orbit and the nares of an orifice (sometimes two or even three), the so-called foramen preorbitale (among amphibians it occurs in certain Stegocephali, such as Trematops, and in reptiles among pterosaurs, also in Parasuchia, Pseudosuchia and certain crocodiles), a certain mobility of the quadrate in some dinosaurs (Telmatosaurus, Claosaurus, both belonging to the Orthopoda),[1] the presence of a horny beak in all Ornithischia.

Ceratosaurus (Theropoda, fam. Coeluridae) from the Lower Cretaceous of Colorado is very remarkable. In that reptile the distal tarsalia coalesce with the already fused metatarsalia, thereby giving rise to a tarso-metatarsus, as in birds. The nasal bone is supplied with a bony ridge, which evidently carried a horny crest (whence the name of the animal—Ceratosaurus), as in the cassowaries (Casuarius), which have on their basal, frontal and especially on their ethmoid bones a casque-like protuberance of osseous tissue, covered with horny integument. In the lower jaw Ceratosaurus has an orifice, as in many birds. The connection of the quadrate with the squamosal was apparently mobile (Versluys, 1910, p. 190). The prefrontals protrude like a gable over the eyes, as in the cassowaries. But the pelvis is not in the least ornithic.

[1] Versluys, 1910, 1912. Among tetrapods a mobile quadrate is met with in nearly all lizards (including the Mosasauria), in snakes and birds. The skull is then called streptostylic.

Are the dinosaurs ancestors of birds? Now arises the question, how is such a similarity between dinosaurs and birds to be explained? The most natural answer would seem to be, that the dinosaurs are the ancestors of birds. Such a solution was formerly actually arrived at by some zoologists and palaeontologists, with the reservation that not all birds have been derived from dinosaurs, but only the keel-less (Ratitae) or ostrich-like birds,[1] and that the ancestors of birds were either the Ornithischia, or Compsognathus. To the writers who derive birds from dinosaurs must be referred Huxley (1868), who claimed that birds owe their origin to forms similar to Compsognathus; then Marsh (1877), Baur, Cope, Menzbier (1887, pp. 86, 88),[2] Mivart (1881) and Wiedersheim (1884) advanced the opinion that keel-less birds were derived from dinosaurs, and keeled birds (Carinatae) from Pterosauria.[3]

But in the present state of our knowledge of the dinosaurs it has become impossible to derive birds from these reptiles: the Saurischia, although their hind-limbs show close affinities with those of birds, cannot be regarded as the ancestors of birds, as their pelvis is not in the least ornithic; the Ornithischia, on the other hand, although having a bird's pelvis, do not exhibit in their anterior extremities any, and in their posterior but slight, affinities with the corresponding limbs of birds.[4] The clavicle is wanting in the dinosaurs,

[1] The last writer holding such an opinion was Steinmann (1908, pp. 218-219). It may be added also, that J. Boas (1914, p. 567) continues to regard the Ornithischia as the ancestors of birds; but the article referred to, dedicated to the phylogeny of vertebrates, is full of antiquated views.

[2] For quotations see Menzbier, 1887, p. 86 *seq.*; Fürbringer, 1902, pp. 728-729.

[3] Owen (1876), however, deriving the keeled birds from the Pterosauria, regarded the keel-less birds as the result of a regressive development of the former.

[4] In most Saurischia neither has the fore-limb any common characters with the wing of a bird; but in some Abel (1919, p. 586) discovers a certain similarity with birds in the structure of the carpus. Namely, in Pachypodosauria and Compsognathidae, the first digit is the strongest, the second the longest, and the fourth and fifth—which are wanting in birds—are small.

and the skull of these reptiles very much differs from that of birds.

Fürbringer (1900, pp. 655-656) points out that in dinosaurs the quadrate is fixed (*i.e.* the skull is monymostylic), while it is free in birds (*i.e.* it is streptostylic). This circumstance alone is sufficient to suggest that we must seek for the ancestors of birds among forms with a free quadrate.

It is true that Versluys (1910, 1912), following Marsh and Nopcsa, discovered that in certain dinosaurs the quadrate is free, and thereby the points of resemblance between these reptiles and birds are increased. Notwithstanding this discovery, however, the writer just mentioned is opposed to the theory of the derivation of birds from dinosaurs: he presumes (1910, pp. 240, 244) that in each the free condition of the quadrate has developed quite independently from the state that we now find represented in Hatteria.

By such steps we have again arrived at the question, how is the similarity between birds and dinosaurs to be accounted for after all, if, as Fürbringer,[1] Gadow (1901), Mehnert (1888), Huene (1907-8, pp. 402-403), Versluys (1910) and Abel (1919, pp. 524, 686) [2] claim, the former are not derived from the latter? All the writers just mentioned explain the similarity between dinosaurs and birds as being due to *convergence*. In this connection, Fürbringer and Mehnert lay especial stress on the resemblances exhibited in the structure of the pelvis (Fürbringer, pp. 1044, 1612) and the hind-limbs.

That view must be accepted.

Origin of dinosaurs and birds. Whence do birds and dinosaurs originate? Fürbringer (1888), one of the leading authorities on the anatomy, palaeontology and classification of birds and reptiles, not only declares against the origin of birds from dinosaurs, but is opposed to their being more or

[1] 1888, pp. 1623-1625; 1900, p. 680; 1902, pp. 726-736.

[2] Among other writers Owen, Vogt and W. K. Parker might also be named.

less closely affiliated. In his opinion (1900, p. 654) dinosaurs diverge from a common stock with crocodiles, somewhere in the proximity of the Rhynchocephalia; birds, as being an extremely specialised group, cannot be derived from any one definite type of reptiles: in their free quadrate and in other respects they possess a certain similarity to primitive Lacertilia (1900, pp. 655-656). The stock from which birds are derived may have been *climbing* Lacertilia (Fürbringer, 1902, pp. 734-735).

Fürbringer thus conceives the course of the transformation of climbing lizards into birds. At first a highly developed capacity for climbing is acquired (he here mentions by way of illustration the case of the young Opisthocomus, as also of other young birds, which possess the capacity for climbing with the aid of their wings), then scales are transformed into feathers, which further involves the acquisition of the faculty of flight and warm blood. The last stage in the process was the development of bipedality (1902, p. 734).

Abel's conception of the origin of birds is nearly the same (1910, pp. 177 *seq.*; 1919, p. 586).

Other scientists derive birds, not from climbing reptiles, but from reptiles that move either by leaping or walking on their hind-limbs. Osborn (1900, pp. 796-797) presumes that the tendency towards becoming bipedal is the most characteristic feature in all, even the most lowly organised, dinosaurs,[1] and thinks that birds trace their origin from primitive *bipedal* dinosaurs.

Nopcsa (1907, p. 234) remarks, that if birds had been derived from arboreal tetrapods and their capacity for flight had been developed before their faculty for walking on their two hind-limbs, it is inconceivable that the fore-limbs alone, and not all four,[2] should be used for flight,

[1] In agreement with this opinion there is a disposition to admit (Huene, 1908, p. 407) that even Stegosauria (of the Ornithischia), which are quadrupeds, are derived from bipedal ancestors.

[2] Recently Beebe (1915) advanced a suggestion that birds had passed through a stage, when they possessed wings on their hind limbs also. This supposition is based on the fact that the pigeon four days old possesses rudiments of 12 primaries and 6 tectrices on the feet; something similar occurs in Archaeopteryx.

the *fore-limbs are less specialised than the hind-limbs*, and that wings, and not patagia, as in Pterosauria and bats, developed in birds. Yet if we direct our attention to the extremities of Archaeopteryx, we shall meet in it with typical bird's feet, with a tarso-metatarsus, a small first digit, an absence of the fifth, etc., while its wings still bear primitive features. Nopcsa assumes that birds have been developed from long-tailed reptiles, which became bipedal and which "clawed" the air with their fore-limbs;[1] in such leaping, dinosaur-like reptiles, the scales on the fore-limbs and on the tail were transformed into feathers, and thereby gave an impetus to flying. This opinion is shared by Versluys (1910, p. 250): he derives both dinosaurs and birds from such Rhynchocephalia (Diaptosauria) as substituted tetrapodal gait for bipedal. Whether such problematical Rhynchocephalia, he says, ought still to be regarded as Rhynchocephalia, or as primitive dinosaurs, is an open question.[2]

Recently Broom (1913) and Huene (1914) and after them Abel (1919), have set about deriving dinosaurs, pterosaurs and birds from the Pseudosuchia.

Pseudosuchia, or pseudo-crocodiles, are a group of extinct, crocodile-like reptiles which flourished in the Triassic. To this group are referred the genera Proterosuchus, Ornithosuchus, Euparkeria, Scleromochlus, Aëtosaurus and some others. Formerly this group was regarded as one of the orders of the sub-class Crocodilia (which was divided into the Pseudosuchia, Parasuchia and Eusuchia). But now Pseudosuchia are considered to be a separate taxonomic unit, the similarity of which to crocodiles is due to convergence. Huene (1908; 1914, p. 22) derives the Pseudosuchia from forms allied to Protorosaurus. We thus encounter here merely a

[1] See illustration in Nopcsa, p. 235.

[2] At the present time there is no inclination to attribute to the Rhynchocephalia a too great phylogenetic value: it is a group that has produced no considerable branch. We may remark, that Palaeohatteria from the Permian of Saxony, which was formerly referred to the Rhynchocephalia, is now regarded as a pelicosaurian (Williston, 1914). Protorosaurus, according to the researches of Williston (1914), does not possess two temporal fossae, therefore it was incorrectly classed with the Rhynchocephalia; the presence of a foramen preorbitale is also doubtful. Abel (1919, p. 451) separates Protorosaurus into a distinct order, Protorosauria. It is remarkable that the bones of this form were hollow.

further development of the above-mentioned views of Versluys.[1]

In Broom's opinion (1913, pp. 631-632) birds are derived from one of the Pseudosuchia, which, having *become bipedal, and having acquired the hind-limbs of* the dinosaur type, assumed arboreal habits and gained a capacity for flight. The Pseudosuchia likewise gave origin to the dinosaurs and the pterosaurs (pp. 630-631). Huene derives (1914, p. 50) from the Pseudosuchia, in the form of separate parallel branches, the Saurischia, Ornithischia, birds, crocodiles (s. str. = Eusuchia), Pterosauria and Parasuchia. Birds have diverged from the Pseudosuchia in the proximity of Ornithischia (p. 42): as to the fate that subsequently befell them, Huene agrees with Broom: the primitive Pseudosuchia were transformed into leaping creatures, somewhat resembling jerboas, and then became Ornithischia. From these jerboa-like Pseudosuchia, prior to their having lost their secondary pectoral girdle, a branch diverged, which became adapted to an arboreal life (similarly to what had occurred in the squirrels, which are derived from leaping rodents of the steppes). By continuous jumping from trees these creatures elaborated a covering of feathers and wings.

But, whatever view of the origin of birds be held, one thing can undoubtedly be inferred from the foregoing account of the various opinions on the subject, and this is that the most striking features of similarity in the structure of dinosaurs and birds are due to convergence, *i.e.* development in a determined direction.

The supposition that both dinosaurs and birds are derived from a common stock, in which the characters common to both had already been combined, must be set aside as being obviously invalid. Let us suppose that birds, Saurischia and Ornithischia, have descended from Pseudosuchia—naturally from various groups of these reptiles, which had respectively acquired the characteristic features of birds, Saurischia and Ornithischia. But if that were the case, by

[1] See preceding note.

what means, unless it were convergence, can the resemblance in the structure of the hind-limbs in certain Saurischia (such as Ornithomimus, see Fig. 26) and birds be accounted for? Whichever group be regarded as the initial one, we are compelled to resort to convergence in order to explain the resemblance between Aves, Ornithischia, Saurischia, Crocodilia and Pterosauria, for the respective similarities of the groups just mentioned intercross, as it were: birds, for instance, in certain respects resemble Ornithischia, in others Saurischia, in yet others Crocodilia, and, lastly, Pterosauria.

As we have already pointed out, the dinosaurs themselves are polyphyletic. Both groups, the Saurischia and the Ornithischia, present points of similarity which have developed independently of one another. To these may be referred, for instance, the ornithic peculiarities in the structure of the hind-limbs in those Saurischia and Ornithischia which progressed by means of their hind-limbs, as well as certain features in the structure of the vertebral column.[1]

A tendency towards the formation of the hind-limbs after the type of the bird's, namely, towards the coalescence of its elements, is indicated likewise in living reptiles: thus, in certain lizards and tortoises the tarsus possesses a large bone, the tarsale proximale, which has been formed by the fusion of several bones. In reptiles is indicated, moreover, the separation of the tarsus into two sections, proximal and distal, between which the principal articulation (intertarsal) of the foot is present.

In chameleons the following features of similarity with birds may be noted—a tendency towards the formation of pulmonary air-sacs, the absence of a urinary bladder and the presence, as in Dromaeus, of a tracheal sac (D'Arcy Thompson).

[1] See Nopcsa (1907, p. 231) on the subject.

6. CROCODILES

Crocodiles with all their typical features suddenly appear in the Lias. Formerly, as was presumed by Huxley, their ancestors were claimed to be the Triassic crocodile-like Parasuchia (Phytosauridae and others) and Pseudosuchia (Aëtosauridae and others); but Koken, Zittel, Williston, Huene and others showed that that was not the case.

As was already indicated by Gegenbaur (1865, 1866), crocodiles exhibit similarities to birds, although, of course, there can be no question of birds having been derived from them.

The most remarkable of these similarities is the structure of the heart, which in both is four-chambered; in connection with which a tendency towards the reduction of the left aortic arch is observed in crocodiles. The carotid arteries of the right and left sides leave the right aortic arch, as in many birds, in the shape of one common vessel.[1] Of all reptiles, the brain of crocodiles most resembles that of birds: the cerebellum is relatively voluminous, covers the rhomboidal fossa and shows a tendency towards a separation, as in birds, into a central and two lateral parts. In the lungs of crocodiles points of similarity to birds may be noted. The ribs of crocodiles, like those of birds, are flat, are supplied with processus uncinati (also found in Rhynchocephalia), and articulate with the vertebrae by means of capitula and tubercula (also found in dinosaurs and pterosaurs). The junction of the coracoid and the scapula at an acute angle recalls similar relations in birds and pterosaurs. The coracoid of crocodiles is like that of the Ratitae. The clavicle, as in majority of the Ratitae, is absent. The ilium is somewhat widened. A certain similarity in the structure of the fore-limbs may be observed (the relative sizes of the ulna and radius, an incipient reduction of the fifth and fourth digits, and especially a tendency towards the coalescence of the elements of the carpus), which involves a similarity in the muscular system (musculi thoracici

[1] In Varanus, Python and Boa the carotids also originate as one common unpaired vessel.

superiores and brachiales superiores; see Fürbringer, 1888, p. 1621; cf. also p. 1615). There is a resemblance in the nervous system (plexus brachialis and lumbosacralis), in the organs of vision and especially those of hearing: the cochlea begins to form a spiral convolution, the cavity of the membranous cochlea is united with the sacculus by means of a narrow canalis reuniens: the utriculus similarly communicates with the sacculus through a narrow canal; a membrane of Corti protecting the auditory cells from above is also present; the middle ear communicates with the air cavities of the surrounding bones; the Eustachian tubes open into the mouth cavity by a common median aperture; and as in birds, especially in owls, a fold covering the external opening of the ear is present. The penis of crocodiles very much resembles that of ostriches (and tortoises).

Similarities to birds are likewise displayed in the structure of the digestive organs: in both classes tonsillae pharyngeae occur at the entrance of the Eustachian tube, the curvature of the stomach resulting in an approximation of the cardiac part to the pyloric is observed, a tendinous plate in the muscular wall of the gizzard is present, as also a long sinuous intestine and a usually bi-lobed liver.

In the structure of the laryngeal cartilages there also is a resemblance: the cartilagines cricoidea and arytaenoidea are well developed. The general structure of the trachea is similar, and in *Crocodilus acutus* it is, as in birds, curved in a loop.

7. FLYING REPTILES

The flying reptiles, Pterosauria, Ornithosauria or Patagiosauria, first make their appearance as scattered remains in the Upper Triassic, reach their culminating point in the Jurassic, and vanish in the Upper Cretaceous without leaving any descendants. They are divided into two sub-orders: the long-tailed Jurassic Rhamphorhynchoidea or Pterodermata, and the short-tailed Jurassic and Cretaceous pterodactyls (Pterodactyloidea or Ornithochiroidea). As

these sub-orders cannot be derived one from another, Abel (1919, p. 554) has promoted them to the rank of orders. The Pterosauria are, thus, also polyphyletic.

The flying saurians in many points exhibit a striking resemblance to birds. There can be no doubt, however, that they are not the ancestors of birds: although, for the purposes of flight, both in the pterosaurs and in birds, use has been made of the modified fore-limbs, yet that modification has been effected by the two in entirely different ways. While in the pterosaurs the flying membrane, devoid of feathers, is supported by the very much elongated fifth ulnar digit, the four first digits in relation to the fifth [1] falling into the background, in the birds essential importance for the skeleton of the wing is possessed by the first three digits, the fourth being rudimentary and that only in the young bird, whereas the fifth has vanished without leaving a trace. The pelvis in pterodactyls is quite unlike that of birds, somewhat recalling the corresponding structure in crocodiles by the presence of a bone, similar to the prepubis of the latter. Yet the striking resemblance of pterodactyls to birds, which we have just noted, is manifested not only in external features, but in the most fundamental structural features.[2]

The skull is set bird-fashion on the vertebral column, in a perpendicular position to the axis of the neck, and is supplied with a beak. The skull possesses no sutures in

[1] The three middle digits are of medium size, free and provided with claws, the first being more or less reduced or even absent. However, Williston (1911) has recently reverted to the opinion of Cuvier, according to which the digit that supports the flying membrane in pterodactyls is the *fourth*, not the fifth. Williston bases this view on the phalangeal formula of the fore-limbs, which in pterodactyls is 2, 3, 4, 4, —; in crocodiles 2, 3, 4, 4, 3; in palaeozoic reptiles, Sphenodon, and the majority of recent lizards, 2, 3, 4, 5, 3. This circumstance renders it very probable that in pterodactyls, as in birds, the fifth and not the first digit is wanting (see also Abel, 1911, p. 599). But even if that were the case, the general scheme in the structure of the organ of flight in birds and pterodactyls remains distinct.

[2] On Pterosauria see M. Fürbringer, 1900, pp. 660-668, 355-364; H. Seeley, 1901. A fuller list of authorities may be found in Zittel, 1911, p. 298; Abel, 1919, pp. 561, 567.

the adult, as in birds. In most birds, on either side of the skull between the orbit and the nasal aperture a preorbital foramen is present, as in all long-tailed pterosaurs (Rhamphorhynchoidea), while in the short-tailed (Pterodactyloidea) it may be absent. Fürbringer (1888, p. 1602) indicates the following points of similarity in the skull of pterosaurs and birds : its relatively large size, a spacious cavity for the brain, a greater or lesser pneumaticity involving reduction in weight of the body, the interrelation of the basitemporal and basioccipital, and the position of the occipital condyle, the size of the orbits and of the nares, the considerable length of the jaws, sometimes toothless and covered, partly or wholly, with a horny integument, the coalescence of the halves of the lower jaw, etc. The general form of the skull reproduces various types of skull exhibited by birds : forms occur with the skull of a woodpecker, or of a heron, or of a cormorant.

In the Upper Cretaceous Pteranodon (Ornithostoma) the lower jaw is articulated with the skull by means of a process with a screw-like surface, as in the pelicans. The sternum is supplied with a more or less developed keel (especially in Ramphorhynchus). The cervical vertebrae of Pterosauria show a certain likeness to those of birds. Although usually the mouth of pterosaurs is armed with teeth, they are quite absent in Pteranodon. The number of sacral vertebrae, which never exceeds three in recent reptiles, in pterosaurs is from (3) 4 to 10, *i.e.* increased, as in birds, and, as in the latter, they are fused with one another. In some forms, such as *Pterodactylus grandis*, and the Lower Liassic Dimorphodon, the proximal series of tarsalia coalesces with the distal extremity of the tibia, as in birds.[1] The fibula is a long, thin, reduced bone, joined to the proximal end of the long tibia, exactly like what is observed in birds. The tibia is considerably longer than the femur, as in birds. The scapula and the coracoid strikingly recall the corresponding bones in birds : their elongated form, reciprocal position, the glenoid cavity for the articulation of the humerus are features similar in birds and pterodactyls, and differ from what we observe in other vertebrates (Fürbringer, 1900, p. 358 ; Seeley,

[1] Seeley, pp. 102-104, 195.

pp. 111-116).[1] The humerus is supplied with a well-developed processus lateralis (probably the place of attachment of the pectoral and deltoid muscles), thereby exhibiting a similarity with Ichthyornis and the Accipitres.

Most bones in pterodactyls are hollow, with pneumatic openings, as is usual in birds. The pneumatic opening in the humerus of the pterodactyls lies in the very same position and has the same size and shape, as in birds. Obviously, these openings were penetrated by the air-sacs of the lungs, and it is to be presumed that the heart in the pterosaurs was four-chambered and the blood was warm, as in birds. This hypothesis was suggested by Seeley and by Haeckel (1866), and both Fürbringer (1888, p. 1638 ; 1900, p. 667) and Gadow approved it. But the most significant similarity is that presented by the brain : in recent reptiles the optic lobes are closely approximated, but in the Jurassic pterosaur Scaphognathus they are separated, owing to the cerebellum meeting the fore-brain, as in birds. Moreover, the cerebellum is supplied with lateral lobes, flocculi, which in existing vertebrates are developed in birds and mammals (rudimentary flocculi occur in crocodiles). In size the brain of pterosaurs is larger than that of reptiles, and approaches that of birds.

We have presented so many features of organisation common both to pterosaurs and birds, that the question arises, are not the pterosaurs birds ? We have already noted the features by which they are sharply distinguished from birds. To these may be added the absence of feathers. That pterosaurs are reptiles is also indicated by the shape of their pre-sacral vertebrae, these latter being procoelous,[2] as is usually the case in reptiles and as never happens in birds, either recent or fossil (in Archaeopteryx the vertebrae are amphicoelous). Then, in birds the quadrate is always freely suspended to the skull, while in pterosaurs, as in most reptiles, it is firmly fixed to it. Lastly, the hind

[1] The dimensions and position of the scapula in birds are connected with the capacity for flight, and correspond with the development of the musculi scapulo-humerales (Fürbringer, 1888, p. 1605).

[2] The caudal vertebrae are amphicoelous.

extremities of pterosaurs are constituted entirely after the type of reptiles. It may be noted that pterosaurs, like true crocodiles and dinosaurs, do not possess clavicles, which are well developed in most birds (furcula).[1]

Very remarkable are some points of similarity in the skeleton between pterosaurs and *mammals*. Thus the femur in Ornithochirus very much resembles that of mammals (Seeley, p. 100). The head of the humerus bears a resemblance to the corresponding part in the fossil reptiles Theriodontia (which in some respects bear a close affinity to mammals), and also to that in Ornithorhynchus (Seeley, pp. 117, 119, 217-218).

The habits of pterosaurs and mammals being so different, it is evident that these points of resemblance cannot possess any adaptive importance. And in any case it cannot be an adaptation to the flight, for in birds and bats the head of the humerus is differently constructed. It is all the more wonderful to encounter in the pterosaurs such a deviation in the direction of mammals.

Again, a series of similarities between pterosaurs and *dinosaurs* may be detected, namely, in the structure of the pelvis and hind-limbs, and in the pneumaticity of bones.

This circumstance induced Seeley some time before Huene to unite the pterosaurs, dinosaurs, birds and crocodiles into the group Ornithomorpha. But, being manifestly polyphyletic in origin, this group cannot be a natural one. Fürbringer (1900, p. 666) holds that pterosaurs and dinosaurs are derived from common ancestors, which were characterised by the following features: the means of progression begin to be restricted to the hind-limbs, bones gradually become pneumatic, squamosal and prosquamosal coalesce, two temporal arches and as many temporal fossae are present, so is the quadratojugal, the quadrate is closely united with the

[1] In some birds, as in the ostrich, kiwi, and some parrots, the clavicles disappear. But this must be regarded as a secondary feature: it is to be presumed that birds devoid of clavicles are derived from those which had possessed them (Fürbringer, 1900, p. 553; 1902, p. 308).

skull by its superior part only, caudal vertebrae are numerous, the primary pectoral girdle is lengthened and is obliquely projected forwards, the secondary pectoral is reduced, the ilium is elongated in the sagittal direction, the hind-limbs have a tendency towards a vertical gait, etc.

Many points of resemblance in structure between dinosaurs and pterosaurs, just as between the pterosaurs and birds, are, *in my opinion, due to convergence.*

Owen was at first disposed (1866-78) to regard the flying reptiles as the ancestors of birds in general. Some writers (Mivart, Wiedersheim, Vogt) were inclined to derive the Carinatae from pterosaurs, and Cope (1867) found in Archaeopteryx an affinity to the Pterosauria. But to this view may be most decidedly opposed the radical difference in the skeleton of the fore-limb of birds and pterosaurs, as well as the mobility of the quadrate in birds and its immobility in Pterosauria (cf. Fürbringer, 1888, p. 1626; 1900, p. 667).[1] In Fürbringer's opinion there are no grounds for admitting that both were even derived from common ancestors, and all similarities in the structure of birds and pterosaurs are due, according to this authority, to convergence, pterosaurs being necessarily classed with reptiles (see above, p. 182, on the origin of birds).

8. THEROMORPHA

Theromorpha (or Theromora) are a small primitive group of extinct reptiles, which existed from the Upper Carboniferous period until the end of the Triassic. They usually are divided into (1) Cotylosauria, to which the pareiosaurs belong; (2) Pelycosauria (including Dimetrodon and others); (3) Theriodontia (Cynognathus); and (4) Anomodontia or Dicynodontia.[2]

[1] Cf. also Gadow, 1901, p. 486.

[2] This classification is borrowed from Zittel-Broili, 1911. Watson 1917, p. 171, distributes these reptiles between two "superordines": Cotylosauria (to which Seymouria, Pareiosaurus and others are referred) and Anomodontia, which include among others the orders of Pelycosauria, Dinocephalia, Dicynodontia, Theriodontia. Williston (1917, p. 420)

In their structure Theromorpha exhibit remarkable points of similarity to mammals, just as dinosaurs do to birds (for which, see above). From the very first they seem to follow the path which is destined to be traversed by mammals.

Of all groups of Theromorpha the one most closely allied to mammals is that of the Theriodontia, and more particularly the sub-order Therocephalia (from the Permian and Triassic). In these animals the teeth are differentiated into incisors, canines and molars. Each tooth, as in all Theromorpha, is implanted in its socket. The lower canines are set in front of the upper ones. The Theriodontia were diphyodont. The quadrate is in many forms (Cynognathus and others) very small, which evidently points to development proceeding in the direction of its reduction and subsequent transformation into the incus, as in mammals. The stapes artienlates with the quadrate, just as it does with the incus in mammals. There is a *long* external auditory passage. The lower jaw possesses a well-developed coronoid process, while the angular and supra-angular, absent in mammals, are small. A wonderful likeness between the lower jaw of the Triassic Diademodon, allied to Cynognathus, and that of the embryo of the marsupial Perameles has recently been observed (Watson, 1914, p. 779). In the Triassic theriodont Gomphognathus (not distantly related to Cynognathus) a separation of the articnlar from the dentary is indicated, a condition which shows a step in the direction of the differentiation of the auditory ossicles, so characteristic of mammals;[1] there was, apparently, another ossicle, corresponding to the stapes or columella; the quadrate was, possibly, free (Petronievics, 1919). The zygomatic arch of theriodonts, composed of the squamosal and jugal, is constructed after the type of mammals. In the South African Triassic Cynognathus the occipital condyle

distinguishes three groups: (1) Cotylosauria, which he refers to the Anapsida; (2) Theromorpha (Pelycosauria and others); (3) Theropsida (Anomodontia, Theriodontia, Therocephalia, Dinocephalia and others). The last two groups are referred to the Synapsida.

[1] As is generally known, the malleus is usually compared with the articular and the incus with the quadrate. According to other views, the malleus and incus together form a homologue of the quadrate

was paired;[1] the skull of this reptile wonderfully resembles in a general way that of a carnivorous mammal; both rami of the mandible coalesce at the symphysis. In *the Theriodontia, the scapula is fused with the coracoid* and carries a ridge (Cynognathus). The massive humerus has a well-developed processus lateralis, two epicondyli and a foramen supracondyloideum.[2] The pelvis is constructed exactly like a mammal's: the ilium, ischium and pubis are joined together at the acetabulum; the ischium and pubis form a wide symphysis. In the anterior dorsal ribs the capitulnm articulates with the centra of the two neighbouring vertebrae (*i.e.* intercentrally). Yet another resemblance is observed in the structure of the carpus and tarsus. The number of phalanges in the fore-and-hind limbs is reduced, being respectively 2.3.3.3.3., as is usual with mammals.

Osborn (1898, pp. 331-332) enumerates about fifteen characters common to theriodonts and primitive Eocene mammals, partly typical of Monotremata (to characters common to theriodonts and monotremes belong the form of attachment of the cervical and thoracic ribs to the vertebral column, and similarities in the pectoral girdle).

These striking similarities, which were discovered long ago, have induced some writers, such as Owen (1876) and Cope (1884; 1896, pp. 87-88), and, quite recently, Osborn (see, *e.g.* 1918, p. 191), M. Schlosser (in Zittel, 1911, p. 349) and Williston (1917), to regard Theriodontia as the ancestors of mammals. However, as Baur (1886), Haeckel (1895, p. 423) and Abel (1919, p. 423) have pointed out, the Theriodontia are too highly specialised to be looked upon in this way. Cynognathus, displaying so much resemblance to mammals, is a large animal, of the size of a tiger, while theriodonts are generally animals of medium size, the most primitive mammals, the Triassic Tritylodon, being quite small.

[1] See Osborn, 1900, pp. 944-945, Fig., on the subject. We may here remark that among mammals the Echidna possesses a single occipital condyle, although bipartite.

[2] The foramen supracondyloideum, normally absent in Primates, is occasionally met with in man in a rudimentary condition. This circumstance has been mentioned by Darwin in his "Descent of Man," chap. i.

In the opinion of Baur, both Theromorpha and mammals are derived from one common stock, from the hypothetical "*Sauromammalia*," being separate branches developing parallel to one another. This opinion was formerly shared by Osborn (1898, 1899, 1900), who derived the Theromorpha and the supposed "Promammalia" (ancestors of Mammalia) from Permian "Sauromammalia." Osborn considered (1898, p. 333) that the skeleton of the Theriodontia possesses all the primitive characters of mammals. Gaupp (1912, p. 239) *holds that mammals have been derived from* reptiles, akin to Rhynchocephalia (Hatteria) and Sauria (lizards and snakes). Abel (1913, p. 423) derives mammals from Cotylosauria, denying their connection with Theriodontia.

Seeley (1896) expressed the opinion, that Anomodontia and Monotremata form one group of Theropsida. There is also a suggestion by Mivart that Monotremata owe their origin to reptile-like ancestors, while Marsupialia and Placentalia descend from amphibian-like progenitors.

Huxley (1864, 1880), Gegenbaur and Haeckel (1866),[1] derived mammals from amphibians. That opinion was followed by Marsh (1898), Kingsley (1899, p. 227; 1900), Fürbringer (1900, p. 647; 1904), Göppert (1901-03).

Fürbringer (1900) maintains that mammals owed their origin to primitive, hitherto unknown, Stegocephali, in which the quadrate was mobile.

Thus, *in my opinion, mammals cannot be derived from* Theriodontia. Therefore, their mutual similarities are due to parallel development (such also is the opinion of Fürbringer, 1900, pp. 643-646). It would seem to me to be more justifiable to derive the Mammalia from forms similar to the Stegocephali, which may have given rise both to reptiles (notably, to Cotylosauria like Seymouria) and to primitive mammals.

[1] In 1895 Haeckel (p. 422) derived mammals from the problematical "Sauromammalia," which are supposed to have constituted a transition from "Proreptilia" ("Protamniota") to "Promammalia."

Other representatives of the Theromorpha, besides the Theriodontia, exhibit similarities to mammals. Thus, in the Permian and Triassic Dicynodon, of the order Anomodontia, the structure of the zygomatic arch, scapula and pelvis is like that of mammals. If we admit that Mammalia were derived from Theriodontia, by what, if not by development in a determined direction, may be explained the similarity of Dicynodon to mammals? In Dinocephalia, lowly organised Permian Theromorpha from South Africa (to which Tapinocephalus, Titanosuchus and others are referred) and Russia (Deuterosaurus) in the region of the ear are displayed remarkable resemblances to what is observed in mammals (Watson, 1914, pp. 779-785). Lastly, in the Pareiosauri, a very lowly organised order of the Theromorpha, we find a development in the direction of mammals, to which the presence of an acromion and the fusion of the pelvic bones testify.

Thus, even if we admit that mammals have been derived from one group of Theromorpha, it follows that the resemblance of the former to other groups of the latter is due to parallel development.

9. LEMURS AND APES

It is now usually acknowledged (Elliot Smith, 1919) that monkeys (Simiae) originated in the Eocene period from animals similar to Tarsius.[1] The Tarsioidei and Lemuroidei have in their turn diverged from the common ancestral stock at the end of the Cretaceous period. Be that as it may, in any case there is at present no inclination to derive the Simiae from the Lemuroidei. And yet these two groups exhibit reciprocal similarities, which have evidently

[1] Tarsius is grouped by some with lemurs, by others with monkeys, while a third opinion (Gadow, S. Smith) places it in a distinct sub-order of the Primates—the Tarsioidei, of the same rank as lemurs and Simiae. In my opinion, Tarsius constitutes a separate order of Placentalia, in which some characters of a very primitive structure are combined with others of high specialisation.

developed independently in both. Among such simian characters in the lemurs Elliot Smith (p. 471) mentions the sulcus centralis in Perodicticus, the tendency of the Sylvian fissure in Nycticebus to unite with the sulcus postcentralis (intraparietalis), as occurs in many representatives of the Cebidae; in addition may be mentioned the remarkable resemblance manifested by Tarsius and Loris in the temporal bone and in the course of the internal carotid, the resemblance between Tarsius and the sub-order of Galagini in the structure of the tarsus, and between lemurs and monkeys in that of the region of the lacrymal bone.

10. KEEL-LESS BIRDS (RATITAE)

Of much importance in the question that interests us is the phylogeny of the so-called keel-less birds, or Ratitae, to which are referred the ostriches, rheas, emus, cassowaries, extinct Madagascar Aepyornithidae, New Zealand moas (Dinornithidae, extinct) and kiwis.

The separation of birds into keel-less (Ratitae) and "keeled" (Carinatae) suggested by Merrem (1813) was first fully elaborated by Huxley (1867), who pointed out a series of radical distinctions between the two.

> The Ratitae are characterized by the following features: the barbules (radii) of the contour feathers are devoid of hooklets; pterylae and apteria are absent (in the adult); the rectrices and remiges are not well developed; there is no coccygeal or oil gland; strong processus basipterygoidei projecting from the body of the basisphenoid articulate with the posterior section of each pterygoid; the articulation of the palatine and pterygoid with the prolongation of the basisphenoid (rostrum) is incomplete or absent (due to the insertion of the vomer [1]); the sutures of the skull are slow to obliterate; the quadrate articulates with the skull by a single facet (not by two); a keel is absent from the usually flat sternum; the coracoid and scapula are ankylosed and small, meet at a very obtuse angle or even

[1] This character (dromaeognathy) is also peculiar to the Crypturidae.

make a straight line; the coracoid is deprived of an acrocoracoid; the scapula has no acromion; the clavicles are rudimentary or absent; the skeleton of the fore-limbs is reduced; the proximal end of the tarsus is late in fusing with the tibia; the ischium does not fuse, or coalesces but imperfectly, with the postacetabular section of the ilium; the syrinx is absent; the shell of the egg (except in Apteryx) is of a peculiar structure; a series of muscles of the fore-limbs and of the pectoral girdle exhibit certain peculiarities (Fürbringer, 1888, p. 1481).

These characters, however, have been shown by Fürbringer to possess no decisive importance, as they are met with, either singly or severally, in different combinations in various groups of the Carinatae, especially in the Crypturidae (the *tinamous*).

One of the most important distinctive features, in Fürbringer's opinion, is the obtuse angle at which the scapula and the coracoid meet; other essential characters are the absence of the acrocoracoid and a different position assumed by the musculi coracobrachiales. In relation to phylogeny much importance is attached to the following primitive characters of the Ratitae: a dromeognathous skull, and the peculiarities of the processus basipterygoidei, the quadrate and the musculature.

Huxley, Gegenbaur, Baur and others regarded the keelless birds as the ancestors of the Carinatae; Mivart, Wiedersheim and Vogt attribute to birds a diphyletic origin, deriving the Ratitae from dinosaurs, and the Carinatae (including Archaeopteryx and Ichthyornis) from pterosaurs or other saurian-like reptiles.

In his monumental work Fürbringer demonstrates (1888, p. 1505) that the group of the Ratitae is not uniform, the differences between the several members of it being very great, and some of the Ratitae being more allied to the Carinatae than to their alleged congeners: thus the kiwi (Apteryx) is more closely allied to the Rallidae (rails, etc.) and the Crypturidae (tinamous), than to the ostrich or rhea. If the Ratitae are to be united in one group, it would be

quite as justifiable to class together all the flightless Carinatae, such as the Aptenodytidae (penguins), the extinct great auk (*Alca impennis*), the extinct New Zealand goose Cnemiornis, the New Zealand flightless "rails" Notornis and Ocydromus, the extinct "pigeons" Dididae (the Dodos) from the Mascarene islands, the New Zealand ground parrot Stringops, etc.

The connecting links between all the Ratitae are due to convergence based on the reduced capacity for flight (*l.c.*, p. 1505). The loss of the power of flight occurred independently in different groups and at different periods: the ostriches appeared first, then came the emu and the cassowaries, and lastly, the rheas. Thus Fürbringer (1902, p. 613) maintains the polyphyletic origin of the Ratitae, and, assuming with T. J. Parker (1882) that the *ancestors of the Ratitae were Carinatae*, he (1888, pp. 1565-67; 1902, pp. 588-592) distributes the Ratitae among a number of orders and sub-orders of the sub-class Ornithurae.

Gadow (1893, pp. 90-114) likewise derives the Ratitae from the Carinatae, recognising the polyphyletic origin of the former. But as progenitors of the keel-less birds he more precisely indicates (p. 99) the ancestors of Tinamiformes (Crypturiformes), Galliformes and Gruiformes, from which the Ratitae had evolved in connection with their loss of the power of flight.

It seems to me more convincing to regard the keel-less (Ratitae) and keeled (Carinatae) birds as two parallel groups, either of which had originated polyphyletically. At the same time, the Carinatae have advanced in their development beyond the stage reached by the Ratitae. The similarity in the structure of both is due to convergence, the disparity being to a great extent the consequence of a more primitive organisation of the Ratitae.

Such an opinion finds support in all we know of the phylogeny of birds, dinosaurs, ornithosaurs, Theromorpha and others, and more particularly in the following reflections.

In the structure of separate representatives of the Ratitae points of similarity are exhibited, not in regard to any one group of Carinatae, but to many, and it is, of course, impossible to believe that any representative of the former should have simultaneously arisen from all the forms of the latter. Thus, in the ostrich may be detected points of resemblance to the Tubinares (petrels, albatrosses, fulmars, etc.), to the Steganopoda (cormorants and pelicans, etc.), to the Palamedeidae (screamers), Anseres (geese, etc.), Pelargo-Herodii (storks and herons), and Otidae (bustards), but especially to the first three groups. As distinguished from ostriches, all these birds are good fliers; and the Tubinares, Steganopoda and Anseres, in addition to that, are very indifferent runners.[1] Yet at the same time the ostrich possesses such primitive characters (the presence of as many as eighteen primaries in the wing, reptile-like coracoids, a pubic symphysis,[2] a short cochlea, peculiarities in the musculature),[3] that it would be inadmissible to derive it from any of the carinate groups named above.[4] The Rheidae display a resemblance to the same groups as do the ostriches, and also to the Gruidae (cranes), Psophiidae (trumpeters), Cariamidae and Crypturidae (tinamous). But, as in the case of ostriches, rheas cannot be derived from any of these groups (Fürbringer, 1888, p. 1512). The allied families Dromaeidae (emus) and Casuaridae (cassowaries) are in some respects similar to the same groups (excepting Anseres) as are the rheas, and also to the Galliformes (gallinaceous birds); as to their phylogeny, what we said of the rheas applies to them. In the Apterygidae (kiwis) and Dinornithidae (moas) most resemblance to the Crypturidae (tinamous) and Rallidae (rails) is manifested,

[1] Fürbringer, 1888, pp. 1508-9.

[2] A pubic symphysis, although of a somewhat different kind, occurs in *Archaeopteryx macrura* (see Petronievics and S. Woodward, 1917, p. 5, pl. I, Fig. 3).

[3] Cf. Fürbringer, 1888, p. 1479, note 3, p. 1510.

[4] In Fürbringer's opinion (1902, p. 621) ostriches come nearest to the ancestors of Pelargornithes, *i.e.* of storks and herons.

and in Fürbringer's opinion (p. 1516) a close relationship is observed here: the moa and the kiwi separated from the common stock close to the branch that gave rise to the rails and tinamous.

Thus, in the opinion of Fürbringer (as also of Gadow), a considerable part of the resemblance between the Ratitae and Carinatae is due to convergence. In this sense this writer (p. 1516, note) regards even the similarities between the kiwi (as well as the moa) and the rails.

From the disuse of wings the Ratitae lost the power of flight. But they had never possessed very efficient wings, derived as they had been from but indifferent fliers. Fürbringer claims (1888, p. 1513) that the ancestors of the emu and cassowaries had never been expert fliers; he says the same (p. 1516) of the ancestors of the kiwi and moa. His general idea is (p. 1505) that, in the primitive small carinate birds from which the Ratitae sprang, the capacity for flight was displayed only very imperfectly. The incapacity of the Ratitae for flight, therefore, is to a certain extent due to the primitive structure of their wings and partly to a reduction of the wings from disuse (in this case we thus also see a determined direction in development).

The relatively long humerus of the rhea and ostrich is a sign of their being on the road towards the acquisition of the power of flight, had it not been for their large size, which testifies to their evolution having run its course and to their being doomed to extinction. We may also point out a manifestation of phylogenetic acceleration in the ostrich: it consists in the feathers of the embryo being distributed in patches on pterylae, leaving the apteria bare, as in the majority of Carinatae, whereas in the adult forms of the Ratitae the whole body is uniformly covered with feathers (down-like).

Besides the incapacity to fly, the Ratitae possess many primitive characters which have already been noted[1] (see

[1] Cf. also Fürbringer, 1902, p. 613.

on the ostrich). We may further add that the position of the musculus coraco-brachialis externus s. anterior in the Ratitae is so primitive as, in the opinion of Fürbringer (1888, p. 1489), to approximate them in that respect to reptiles, and to prevent us from deriving those characters from the corresponding structure of the Carinatae. All these primitive features in the Ratitae, in my opinion, make it impossible to regard them as the descendants of the more highly developed Carinatae.

Moreover, the Crypturidae, Galliformes and Gruiformes are so highly organised and well differentiated that it is simply impossible to make them or allied extinct forms the ancestors of the Ratitae. It thus remains to seek for the ancestors of the Ratitae among the *ancestors* of the Galliformes, Gruiformes, etc., which would be endowed with characters revealing a much lower degree of specialisation.

The large bodily size of the representatives of the Ratitae testifies to their having traversed a long route in evolution,[1] and this circumstance, in connection with a series of primitive characters in structure, has induced Fürbringer (p. 1504) to set the time of the divergence of the Ratitae from the Carinatae very far back; possibly as far back, he says, as the commencement of the Mesozoic period. But can one speak of carinate birds as existing at that distant period ?

We have already pointed out that the Ratitae are polyphyletic. This peculiarity of theirs affects not only forms widely distant from, but also closely allied to each other in the system. The African ostriches (Struthio) and the South American rheas [2] display many common characters, not only in outward form, but also in anatomical structure ;

[1] Large-sized birds are, in general, superior in organisation, and more differentiated, than small ones. This law, first established by Fürbringer, in relation to birds (1888, pp. 991-995) and applied by him to mammals, was further developed by Depéret (1907). In Fürbringer's opinion (p. 993), the progenitors of birds were smaller than Archaeopteryx, but larger than the small and medium-sized Passeriformes.

[2] Fürbringer regards them as representatives not only of various families, but even of distinct orders.

thus in both the humerus is relatively long, but at the same time "a careful anatomical examination exhibits such essential diversities in their internal structure that there can be no thought of regarding them as being related by blood" (Fürbringer, 1902, p. 622; see also 1888, pp. 1439-1443).

Following on the researches of Pycraft (1900), the Ratitae have lately been united by many (see, for instance, Bianchi, 1913, pp. xxviii-xxix; Zittel, 1911, p. 319) with the tinamous into one group—the Palaeognathae or Dromaeognathae. The tinamous (Tinamidae or Crypturidae) compose a fairly extensive family of South and Central American birds (about 65 species) similar in external form to partridges, *and possessing a keel on the sternum.*

But Fürbringer (1902, p. 672) opposes such a union. It does not seem a judicious one to me either: the similarity between the Ratitae and the tinamous is due to convergence (development in a determined direction). In fact, in the tinamous similarities not only with Ratitae, but with different groups of Carinatae are manifested. These similarities must in both cases be attributed to convergence.

The foregoing leads us to the following conclusions:

(1) The Ratitae are not derived from the Carinatae, neither are the latter derived from the former.

(2) The similarity between the Ratitae and Carinatae is due to convergence.

(3) Not only birds, as a class, but Ratitae and Carinatae, taken separately, are polyphyletic groups.

Thus, in the class of birds manifestations of convergence are wide-spread. Whenever convergence is met with, development is subject to law.

11. MONOCOTYLEDONS AND DICOTYLEDONS

The relations between the keel-less and keeled birds are exactly the same as subsist between the monocotyledons

and dicotyledons. Just as formerly the Ratitae were regarded as being the ancestors of the Carinatae, so the *monocotyledons* were looked *on as* the progenitors *of the* dicotyledons. But among recent writers, Wettstein (1911), Lotsy (iii, 1911, pp. 438, 624) and Kuznetzov (1914) most *decidedly oppose this theory.*

Just as the Ratitae have been alleged to be derived from the Carinatae, so do many writers (Strasburger, Delpino, Flahault, Hallier, Arber, Parkin, Sargent, Lotsy, *iii*, 1911, pp. 616 *seq.*; Berry, 1920, p. 370), at present derive the monocotyledons from the dicotyledons. To this latter *opinion Wettstein is disposed to adhere, but only on the* assumption that the divergence of the monocotyledons from their congener's stock had occurred at a very early period.

It appears to me that, just as the Ratitae and the Carinatae are two parallel branches, which have independently *developed, so are the monocotyledons and dicotyledons two* parallel stems, the mutual similarities of which are due to convergence.[1]

> Characters of monocotyledons are met with in a series of dicotyledons:[2] a single cotyledon occurs in certain Nymphaeaceae, Berberidaceae, Ranunculaceae, Piperaceae, Umbelliferae, Primulaceae (in Cyclamen, for instance).[3] Monocotyledonous plants having two cotyledons are unknown, yet recent researches have disclosed that monocotyledons do essentially have two cotyledons, one of which either atrophies or is transformed into the first green leaf, or else the single cotyledon is the product of the coalescence of two separate cotyledons.[4]
>
> "Monocotyledons," says Kuznetzov (1914, p. 556), "are those dicotyledons which have, in one way or

[1] Parallelism in the development of the monocotyledons and the dicotyledons has been recognised by Nägeli, Kny, Warming, Engler, Nawaschin, Haeckel (i, *1894*, p. 372), Velenovsky, *1910*, pp. 281-282.

[2] Lotsy, iii, 1911, pp. 503-504; N. I. Kuznetzov, 1914, p. 556 *et seq.*

[3] Cf. N. I. Kuznetzov, pp. 451-453.

[4] As in the dicotyledons Ficaria and the Nymphacaceae, which possess but one cotyledon, formed from the union of two.

another, acquired an outwardly single cotyledon." [1] Not infrequently, among dicotyledons, flowers with trimerous cycles are met with, as in *Cabomba aquatica* of the Nymphaeaceae, in magnolias, in the Lauraceae. Berberidaceae, Polygonaceae, etc. On the other hand, the flowers of the monocotyledons are not all trimerous; thus, for instance, the pond-weed Potamogeton possesses a tetramerous flower. The anatomical structure of the stem typical of monocotyledons (the closed vascular bundles without cambium scattered irregularly among the tissues) occurs in certain dicotyledons of the orders Ranales, Piperales, Centrospermae, etc. In monocotyledons the radicle usually disappears, and in its place secondary permanent roots are developed, which fail to exhibit a latitudinal secondary growth; while in dicotyledons the radicle becomes the permanent root of the plant, and is endowed with secondary growth. In certain dicotyledons, however, the radicle does not develop, being replaced by lateral and accessory roots, as, for instance, in *Ficaria ranunculoides* of the Ranunculaceae.[2] On the other hand, monocotyledons are met with in which the radicle develops into the permanent root of the plant. In the leaves of monocotyledons the venation is parallel or acrodromous, in those of dicotyledons for the most part it is netted. Bnt in certain monocotyledons cases of netted venation in the leaf occur, as, for instance, in many Aroideae, in the Dioscoraceae, in the genus Paris of the Asparagaceae; and, on the other hand, a parallel venation is met with in some dicotyledons.

The monocotyledons display the greatest resemblance to the order Ranales, one of the most primitive of the Dialypetalae (Polypetalae), which is close to the Monochlamydeae [3] (the Ranales include the families Berberidaceae, Ranunculaceae, Nymphaeaceae, etc.). The similarity between the monocotyledonous Helobiae (to this

[1] See also the investigations of Hill.

[2] This plant (*F. ranunculoides*) has one cotyledon produced from the union of two separate ones.

[3] Kuznetzov (1914, p. 626) regards the Polycarpicae as one of the sub-classes of his class of Protanthophyta (the other class being the Monochlamydeae). The limits of the Polycarpicae are variously defined by different writers: see on the subject Kuznetzov, 1914, p. 399; we follow his classification. Ranales is one of the orders of the sub-class Polycarpicae.

order belong the Alismataceae, Butomaceae, Hydrocharitaceae, Potamogetonaceae, Naiadaceae) and the dicotyledonous Nymphaeaceae is so great that some botanists (Lyon, 1901; Cook, 1902; Schaffner, 1904) have attempted to class the Nymphaeaceae with the monocotyledons. This is analogous to the transposition of the Crypturidae (tinamous) from the Carinatae to the Ratitae.

Kuznetzov (1914, pp. 401, 567), on the contrary, judging from the structure of the flower and the apocarpous gynoecium,[1] believes that the Helobiae might even be referred to the Polycarpicae.

The points of resemblance between the Nymphaeaceae and the monocotyledons are the following: the flowers are sometimes (as in the sub-family Cabomboideae) trimerous, the cotyledons are sometimes united, thereby forming but one cotyledon; the radicle is more or less reduced; the fibro-vascular bundles are distributed in the stem according to the monocotyledonous type.

The Berberidaceae of the same order likewise exhibit remarkable points of resemblance to monocotyledons. In many, one cotyledon (produced by the union of two) occurs, the fibro-vascular bundles are scattered in the tissues of the stem; in Podophyllum the rhizome branches sympodially, the floral shoot is monopodial, as in Polygonatum of the monocotyledons; in Berberis the flowers are of the trimerous type (Kuznetzov; Lotsy, iii, pp. 593-594).

We repeat: the monocotyledons display a similarity not only with the Renales, but also with other orders of dicotyledons, such as the Piperales, Centrospermae, Polygonales.

The order Piperales, comprising according to Wettstein only one family, the Piperaceae,[2] belongs to the Monochlamydeae. The flowers are entirely devoid of perianth, or the perianth is rudimentary. The position of the family in the system is uncertain. In this case we are particularly interested in the points of similarity between the Piperales

[1] The gynoecium is said to be apocarpous if it consists of free, not coalesced, carpels, as, for instance, in the magnolia.

[2] Engler ("Syllabus") includes in the Piperales the Saururaceae, Piperaceae, Chloranthaceae, and Lacistemaceae, and places this order in the vicinity of the Verticillatae.

and the monocotyledons. They are as follows: the leaves are not infrequently acrodromous; the type of the structure of the flower is trimerous (the number of stamens owing to reduction may be two, as, for instance, in *Piper nigrum*; the stigma is three-lobed, which attests to the pistil having been formed from the union of three carpels); in many species the vascular bundles, as in monocotyledons, are scattered without order, although endowed with the faculty of latitudinal secondary growth, as in dicotyledons. Hallier, followed by Arber and Parkin, holds that the absence of perianth in the Piperales is a secondary phenomenon, as the perianth they formerly possessed was subsequently lost, and he derives Piperales from the Polycarpicae. Lotsy (iii, p. 514), concurring in this opinion, went further, in deriving from the Piperales the Aroideae (Spadiciflorae). Kuznetzov (p. 402) does not admit that the origin of the Piperales from the Polycarpieae has been proved, but shares the opinion as to the affinity of Piperales with the Spadiciflorae, and even suggests placing the Spadiciflorae among dicotyledons, namely, among the Monochlamydeae (pp. 568, 638). Since Kuznetzov derives the Helobiae from the Ranales, he consequently admits the polyphyletic origin of the so-called monocotyledons;[1] this view is shared by Hallier and Lotsy (iii, 1911, pp. 624, 864), as also by Busch (1915, pp. 404-405, 508-509).

The order Polygonales, with only one family, Polygonaceae, is also referred to the Monochlamydeae. In some of the plants belonging to this order, as in the Californian Pterostegia, the flowers are constructed on the typical plan of monocotyledons, being trimerous and possessing five cycles; the perianth is composed of two cycles, the gynoecium is trimerous. On the same trimerous type are constructed the flowers of the minute polar polygonaceous *Koenigia islandica*, as also of the rhubarb (Rheum) and sorrel (Rumex).

The Centrospermae (of the Monochlamydeae) include the Chenopodiaceae (Atriplex, beet, salt-grasses, Haloxylon), Cactaceae, Carophyllaceae and others. In certain Centrospermae (as in Chenopodiaceae, Amarantaceae and others) in the xylem of the stems and roots rings are some-

[1] Cf. also Kuznetzov, pp. 580-581.

times produced, constituted after the type of monocotyledons, as in Dracaena: the cambium originally laid down in the fibro-vascular bundles ceases to act, and a secondary cambium is formed in the fundamental tissue, which proceeds to deposit xylem and phloem anew (Kuznetzov, 1914, p. 329).

We thus meet with characters of the monocotyledons, not in one family only of the dicotyledons, but in various families belonging to different groups, which are, it is true, not very highly organised (Monochlamydeae and Polycarpicae).

Miss Sargant derives both the dicotyledons and monocotyledons from an imaginary ancestor, the flowers of which were supposed to be composed on the plan of the magnolia. Kuznetzov's view does not differ much from the preceding (1914, pp. 581-3): the monocotyledons, in his opinion, owe their origin, not to the dicotyledons, but to the primitive angiosperms ("Protanthophyta"), which combined the characters of both, this condition being embodied in both the Monochlamydeae and Polycarpicae. According to this botanist, the monocotyledons are at the least diphyletic: from the Monochlamydeae were derived the Spadiciflorae through the medium of Piperales, the Polycarpicae giving rise to all the remaining monocotyledons, with the Liliiflorae at their head, through the Ranales [1] and Helobiae.

We cannot concur in the opinion that the Monochlamydeae and Polycarpicae are Protanthophyta, *i.e.* primitive angiosperms in which the characters of the monocotyledons and dicotyledons are combined. Neither among the Monochlamydeae nor the Polycarpicae can be found a single representative in which all the characteristic features of

[1] To the Ranales Kuznetzov (p. 432) refers the families of Menispermaceae, Lardizabalaceae, Berberidaceae, Ranunculaceae, Nymphaeaceae and Ceratophyllaceae; and to the Polycarpicae those of Anonales, Ranales, Aristolochiales, Nepenthales, Rhoeadales, Helobiae (monocotyledonous!) and Hamamelidales (p. 633).

both monocotyledons and dicotyledons occur together; only certain *combinations* of characters of either of these groups may be met with in some genera, but that cannot entitle us to regard the Monochlamydeae and Polycarpicae as generalised groups and ancestors of monocotyledons and dicotyledons. On the whole, it is difficult to imagine an organism in which the characters of the monocotyledons and dicotyledons might be combined. This is one of the cases frequently recurring in the history of phylogenetic constructions: in our endeavours to trace the phylogeny of two groups we often fail to find any transitional forms in a fossil state between the two, and are therefore induced to resort to the creation of ideal ancestors, to which we are obliged to attribute either diagrammatic, pale and lifeless characters, or such a combination of features as, by embracing all the characteristic properties of both groups, precludes thereby the very possibility of the existence of such progenitors; such is actually the case with the imaginary "protanthophytes," on which the characters of both monocotyledons and dicotyledons have been lavished.

Arber and Parkin (1908) agree with this opinion, and affirm that there never existed on earth such a primordial angiosperm, all the organs of which were *equally* primitive.

On the strength of the foregoing considerations we are not disposed to derive the monocotyledons either from any of the dicotyledonous branches, such as the Ranales, for instance, as does Wettstein, nor from two groups of the dicotyledons, the Piperales and the Ranales, as is suggested by Kuznetzov, who attributes to the monocotyledons a diphyletic origin from these two.

We presume that the similarity between the monocotyledons and the Ranales (namely, the same plan in the structure of the flowers, the structure of the carpels and fruits, the mode of formation and development of the embryo-sac, the phenomenon of double fertilisation—all of which are characters not present in plants other than the

monocotyledons and dicotyledons) is due to parallelism in development, and that the monocotyledons and dicotyledons *have separate roots. They are two branches* developing parallel to one another, and, while in their lower representatives, as far as these are known, monocotyledons are higher in the scale than the lower dicotyledons, the higher representatives of the latter are in general of a more complex structure than the highest monocotyledons. The evolution of the dicotyledons has, on the whole, advanced beyond that of the monocotyledons.

Karsten (1918) also finds it impossible to derive Monochlamydeae from Polycarpicae.

It is remarkable that the first known monocotyledons come from the Lower Cretaceous, namely, from the Gault of Portugal (Valanginien) and North America (Upper Potomac beds). They occur *contemporaneously* with the dicotyledons.

Like the monocotyledons, the dicotyledons are polyphyletic. According to Kuznetzov (1914, p. 193) the angiosperms at their first appearance (as far as is known, in the Cretaceous period) " may have arisen polytopically, in different parts of the globe, and, consequently, from diverse types of antecedent gymnosperm or protanthophyte plants."

Of the anthophyte orders, the Verticillatae (Casaurinaceae), Piperales, Salicales, Juglandales, Anonales are very ancient, primitive branches, which cannot be derived one from another. The Salicales used formerly to be united with the Myricaceae, Juglandaceae, Betulaceae and Fagaceae in one group Amentaceae, on the grounds that the common type of their inflorescence is the catkin. But in all other respects these families are morphologically distinct, and cannot be derived from one another.

The Monochlamydeae, according to Kuznetzov (1914, p. 285), " have more than once arisen, both morphologically and geographically, from the Archegoniata. Their origin is

polyphyletic, not monophyletic."[1] The Verticillatae, Piperales and all the so-called Amentaceae have each an independent origin.

12. SOME SUPPLEMENTARY EXAMPLES

We shall now take a few supplementary examples illustrating convergence, beginning with cases of similarity in diverse systematic groups, and concluding with an examination of the formation of identical organs in various groups.

1. At the very time when in North America the Equidae were being evolved, forms of the order Litopterna were being elaborated in South America in the plains of the Argentine. The latter are extinct ungulates, in many respects recalling horses: they had also lost the lateral digits of their limbs, and for progression made use of the *median digit; their extremities and neck were likewise* lengthened, and in the former the ball-and-socket joints, by which movements in all directions could be accomplished, were being gradually supplanted by pulley joints, which restricted their limbs to being moved only backwards and forwards; their teeth lengthened and grew more complex (although no cement was present). This group was extinct in South America before the arrival of horses. The Litopterna, or pseudo-horses, thus copied the horses in many ways.

The same course (as to limbs and teeth) as in horses was followed in the evolution of camels in the New World, and of deer, antelopes, sheep and oxen in the Old.

2. The Titanotheria, extinct (Lower Oligocene) American perissodactyles, are divided into two branches, which develop parallel to each other (Osborn, 1910, p. 212).

[1] The view according to which Monochlamydeae are degraded forms which have developed from more highly organised dicotyledons that are pollinated by insects (Hallier), is arbitrary; palaeontology disproves it. Monochlamydeae now constitute about 15% of all species of plants, while in the Cretaceous flora they numbered 61-64%. Sympetalae form 48% at present: these were only 4-5% in the Cretaceous period (Kuznetzov, p. 369; *Wettstein, 1911*).

3. The Ichthyosauria, both in external and internal features, display many points of resemblance to the Cetacea, notably dolphins: they have a large head with nostrils placed far back, a very short neck, fins in the shape of flippers, a dorsal dermal fin; the pelvis, sternum and clavicles are reduced, etc.

4. The tail-less Amphibia provided with a tongue (Phaneroglossa) fall into two groups, the Arcifera and the Firmisternia, *each* of which represents two series, distinguished by the shape of the transverse processes of the sacral vertebra: in the one they are expanded, in the other cylindrical (Gadow, 1901, p. 139; Terentjev, 1923, p. 33). Thus development in both groups followed a determined and identical course.

5. Watson (1917) divides the Stegocephali into three groups, *i.e.* Labyrinthodonti, Phyllospondyli, and Lepospondyli, the earliest representatives of each of which differ from one another in the same degree as do the latest. These groups develop parallel to each other (Watson, p. 181).

6. One of the most remarkable cases of parallel development is exhibited by the diurnal birds of prey and the owls. The first belong to the order Falconiformes, the second to the Coraciiformes (which includes, among others, the goatsuckers, swifts, humming-birds, hoopoes and woodpeckers). These orders are very widely separated, being referred to distinct groups. Yet owls manifest, not only in external characters but in internal structure, many points of resemblance to the Falconiformes, *i.e.* in the muscles of the limbs, in the crop, in the tarso-metatarsus. The anatomical discrepancies between the two, however, are so great, that any union between the owls and the Falconiformes is quite out of the question: the owls are most akin to the goatsuckers. Such is the authoritative opinion of Fürbringer (1888, p. 1554; 1902, p. 690) and of Gadow (1893, p. 240; see also Bianchi, 1913, pp. xxxiii-xxxiv).

Let us now proceed to examine the phenomena of convergence manifested in the system of separate organs. Some of the examples given below may serve as an excellent illustration of the operation of the principle of phylogenetic acceleration (the placenta, autostyly, organs of sight, the formation of seeds).

7. The placenta, or the organ by which the embryo is connected with body of its mother, was independently formed in various groups of animals : in Polyzoa, in Peripatus, in certain insects and scorpions, in the Tunicata, in certain sharks, in certain marsupials and in all placental mammals.

In the Marsupialia the first indication of a placenta is exhibited in the koala (Phascolarctos), of the Phalangeridae, in which the allantois is closely applied to the chorion over a very restricted area ; the same feature may be observed in certain representatives of the kangaroos (Macropodidae), namely, in Aepyprymnus and Halmaturus. But in the marsupial Perameles, which belongs to quite a distinct suborder from the above-mentioned forms (namely, to the Polyprotodontia), a true placenta is met with : the allantois is so intimately connected with the mucous membrane of the uterus that it may be regarded as an allantoic placenta. Besides a placenta of the kind described above, both in the marsupials (Dasyurus) and the placentals (in the horse, the pangolin, etc.), a vitelline placenta sometimes occurs (when the vessels of the yolk-sac are intimately contiguous with those of the uterus (Weber, 1904, pp. 287-289; Meisenheimer, 1921, p. 627).

But it may be urged that some marsupials possess a placenta, because they gave rise to the Placentalia. Such was, indeed, the opinion formerly prevailing. But in this case the same thing happened which arose in the question of the mutual relation of the monocotyledons and dicotyledons, and keel-less and keeled birds. Some authorities now derive the Marsupialia from the Placentalia.

Thus, for instance, in the opinion of Broom (1910, p. 766) *the marsupials now living owe their origin to Placentalia* in the Cretaceous period, while the Multituberculata (=Allotheria: Tritylodon, Plagiaulax and others, from the Trias

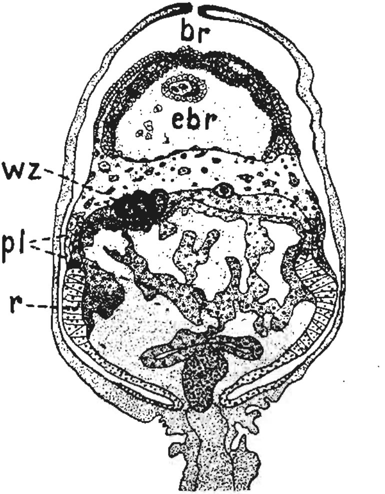

FIG. 27.—Section through the embryo and placenta of Salpa pinnata.
br. brood-chamber; *ebr.* embryo; *pl.* placenta; *r.* ring thickening of placenta; *wz.* migratory cells.
(After Brooks. From J. Meisenheimer, "*Geschlecht und Geschlechter im Tierreiche*," i. Jena, 1921, G. Fischer.)

to the Lower Eocene), which Osborn (1910, p. 518) and Abel (1919, p. 712) regard as archaic marsupials, are one of the branches of the Monotremata. But Broom adduces no proofs to support his claim. Everything in the anatomy, embryology and palaeontology of mammals inclines us to share Abel's opinion (1919, pp. 710-711): the Monotremata,

Marsupialia and Placentalia are three parallel branches which have arisen independently of one another. The pouch of the Marsupialia has apparently been independently evolved in different members of that group (Winge). The teeth of the Marsupialia radically differ from those of the Placentalia in the absence of a true diphyodont dentition (Abel, 1919, p. 711). The placenta in the Marsupials and the Placentalia are thus two independent structures.

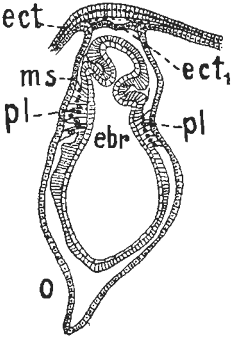

FIG. 28.—Placenta in *Plumatella* (a polyzoon).

ebr. embryo; *ect.* ectoderm of the body wall of the colony; *ect_1.* ectoderm of ooecium; *ms.* mesodermic peritoneal epithelium; *o.* ooecium; *pl.* placenta.

(After Braem. From J. Meisenheimer, "Geschlecht und Geschlechter im Tierreiche,"). Jena, 1921, G. Fischer.)

Something similar to a vitelline placenta has been described by Giacomini (1891, 1906) in the viviparous lizard *Gongylus ocellatus*, as also in the lizard *Seps chalcoides* (cited from Meisenheimer, 1921, p. 626, Fig. 629).

Of the placenta in the sharks we have spoken already (chap. ii). In some of the Tunicata, namely, in the Salpae, an organ has been described, which both morphologically (C. Saint-Hilaire, 1912, p. 99) and physiologically resembles the placenta of Mammals (see Fig. 27).

A placenta has been described[1] in the case of phylactolaematous Ectoprocta among the Polyzoa, *e.g.* in Plumatella and Fredericella. It is well exemplified in the latter genus; in this instance not only an intimate coalescence of the ectoderm of the embryo with the mesoderm of the mother takes place, but the cellular elements of the embryo are

[1] F. Braem, 1897, 1908, quoted from Meisenheimer, 1921, pp. 635-6, Fig. 635.

so closely interwoven with those of the mother that it is impossible to draw a dividing line between them (see Fig. 28).

A placenta has been described from the singular African viviparous insect Hemimerus, a representative of a distinct group, allied to the Orthoptera. The placenta is formed at the expense of the follicular epithelium of the ovary surrounding the developing egg (Heymons, *1909*). In a like manner, in the viviparous species of Peripatus (such as *P. edwardsi*), we find a placenta and an umbilical cord, which connects the embryo with the parent. In the species named, the embryo is developed in the uterus ; the ectoderm of the embryo adjoining the uterus, conjointly with the wall thereof, gives origin to the placenta, while part of the body of the embryo, which connects it with the body of the mother, is transformed into an umbilical cord. A structure resembling a placenta is met with in the scorpions *Scorpiops hardwicki* and *Hormurus australasiae* (Pawlowsky, 1917, pp. 199, 230)[1] as also in some viviparous flies (Cholodkowsky, 1907, *1908*).[2]

8. The vertebral column with ossified vertebrae has been *independently* developed in several groups of vertebrates. Setting aside the Selachii, in which bones are absent, and the same mechanical result is obtained by the calcification of cartilage, we witness the formation of ossified vertebrae in Crossopterygii (*i.e.* Polypterus), in Teleostei (in which the Holostei are included), and, finally, in amphibians. Of those among the Stegocephali, some forms, namely, Phyllospondyli, to which, among others, is referred the Upper Carboniferous and Permian Branchiosaurus, possess a notochord without constrictions : it becomes enclosed in a tube produced by a double series of slender paired ossifications (basidorsalia, basiventralia). In other Stegocephali,

[1] In *Heterometrus cyaneus* (= *Scorpio indicus*), according to the researches of Pawlowsky (1917, p. 223), there is neither an embryonic nor a maternal placenta.

[2] To these investigations of Cholodkowsky my attention was kindly drawn by Pawlowsky.

as, for instance, in the Lower Carboniferous Loxomma, Triassic Mastodonsaurus and others, fully ossified amphicoelous vertebrae are met with. Finally, the last series, leading from forms with vertebrae that are not fully ossified to those in which they are, we find in the tailed amphibians, Urodela.

Opisthocoelous vertebrae are met with among fishes only in Lepidosteus. In the amphibians we find them in certain Salamandridae (Desmognathini) of the tailed group, and in the Pipidae, Discoglossidae and certain tropical Pelobatidae among the tail-less forms. It is remarkable that the *development of the articulation between two adjacent vertebrae* proceeds in all the above-mentioned forms in one and the same manner: the projecting knob is formed as follows—the intervertebral cartilage splits into two parts, an anterior, concave part which unites with the posterior face of the preceding vertebra, and a posterior, convex part uniting with the anterior face of the succeeding vertebra. In this manner is obtained the articular surface.

9. Nature has made three attempts to create among vertebrates forms with an autostylic skull: first in the Holocephali, then in the Dipnoi, and finally, in the Tetrapoda. The first two attempts ended in failure; both the Holocephali and the Dipnoi are terminal branches which have ceased to develop.[1]

Twice endeavours have been made to produce fish with gill covers: once in the Holocephali, and subsequently in the Dipnoi and the Teleostomi.

10. Willey (pp. 109-110) drew attention to the fact that the muscular stomach (or, to be more exact, a modification of the pyloric end of that organ), similar to that of the bird, developed in two very widely separated groups of fishes: in the grey mullets (Mugil) and herrings of the

[1] It is possible that the skull was also autostylic in the Palaeozoic fishes Coccostei.

Dorosomatidae (the representative of the family being *Dorosoma*, or Chatoëssus). It is remarkable that certain grey mullets and Dorosoma have adipose eye-lids. To the above may be added another example: in the South American fresh-water fish *Bivibranchia protractila*, of the group Characinoidei, a powerfully developed muscular stomach and an adipose eye-lid are also met with (Eigenmann, 1912, pp. 258-260, pl. xxxiii). All the above are fishes inhabiting shallow waters with a sandy bottom. Willey on the coasts of Ceylon used to catch Dorosoma and Mugil simultaneously. All the species mentioned belong to different orders.

11. The *luminous or phosphorescent organs, enigmatic as* to function and origin, develop independently in the most diverse groups of marine fishes, as in sharks (Spinax and others), in the Stomiatidae, Scopelidae, Antennariidae and others. Being, apparently, modified dermal slime-secreting glands, and not connected in any way with the perception of light, these organs sometimes, however, manifest in structure a wonderful resemblance to the eye.

Electric organs also appear quite independently in the most diverse fishes, both marine and fresh-water: in skates (Torpedo, certain species of Raia and others), in the electric eel (*Gymnotus electricus*), in Mormyridae, in *Malapterurus electricus*, and in certain Uranoscopidae.

12. In the remarkable Central American "four-eyed" fish *Anableps tetrophthalmus*, of the family Cyprinodontidae, the eyes are divided by a horizontal band of the conjunctiva into an upper and lower portion; the fish swimming on the surface of the water makes simultaneous use of its eyes for vision in the air and water. We find a wonderful analogy to the above in beetles. In the whirligig beetles, Gyrinidae, which swim on the surface of the water, the eyes are, exactly in the same way, divided into an upper and lower portion, enabling the beetle to look down in water and

up in air. Thus the whirligig beetles are supplied on each side with a pair of perfectly distinct eyes.[1]

I take this opportunity of observing that the condition of the eyes, as they occur in Gyrinidae, is a result of evolution in a determined direction. In beetles (see G. G. Jacobson, "Coleoptera of Russia and Western Europe," part i, St. Petersburg, 1905, p. 5, Russ.) the shape of the eyes is generally round or oval, sometimes with a more or less deep indentation of the inner margin (as in Cerambycidae); it happens that this indentation is so deeply inserted in the eye that the latter is divided into two sections (Tetrops, Oxylia, Opsilia). An extreme manifestation of this tendency towards the duplication of the eye is exhibited in Geotrypes and Gyrinus, where the organ of sight is divided into two portions by the deep projection of the sharp margin of the clypeus.

13. The hymen (or virginal membrane), a rudimentary and totally useless organ,[2] is independently developed in different groups of vertebrates: it has been described in certain sharks, among Teleostei in the "miller's thumb," *Cottus gobio* (Guitel, 1913, p. 467), and, finally, in mammals (certain marsupials, rodents, ungulates, lemuroids, primates). It must be noted that while in sharks and mammals copulation takes place, that is apparently not the case with the miller's thumb.

14. Among the most remarkable cases of convergence mentioned also by Darwin, is the structure of the organs of sight in various types of animals. In the protozoon *Erythropsis agilis* of the Dinoflagellata, the reddish-brown

[1] Jacobson has drawn my attention to the fact that imagos of mayflies have the eyes divided into two differently constructed portions. See G. Jacobson and V. Bianchi, "Orthoptera and Pseudoneuroptera," St. Petersburg, 1905, p. 859, Fig. (Russ.).

[2] It is remarkable that in the young females of the mole (in England they are born in May) the vagina remains entirely closed until the following spring; in April, in the eleven-month-old female, an opening leading to the vagina is formed across the perineum. After parturition, in autumn, the entrance into the vagina is closed again. It should be noted that a closed vagina is a normal stage in the development of the human embryo, and in the marsupial Perameles the unpaired vagina closes again after copulation. (See Wood-Jones, 1914.)

pigment spot is already supplied with a spherical refracting body, analogous to the crystalline lens (Fig. 29). To the same family of Gymnodinidae belongs Pouchetia, which has a kind of cornea, a lens and a pigment spot (Fig. 30). Eyes with a lens are independently met with in different groups of animals, such as annelid worms, Arthropoda, Cephalopoda, vertebrates, etc. The complex eyes of the Cephalopoda, much resembling those of vertebrates, are very remarkable: in both cases, besides the lens, we meet with a retina, cornea, iris, supplied with muscles, ciliary process (to which in the Cephalopoda an epithelial one corresponds), and, finally, in some there are eye-lids. In vertebrates the retina is pierced by peculiar Müllerian fibres, to which in Cephalopoda supporting cells in the second[1] ganglion correspond (Lenhossek, 1896). (Notwithstanding such similarities, very marked differences are observed in other particulars: thus, in the Cephalopoda the layer of retinal rods lies inside the retina, whereas in the vertebrates it lies outside.)

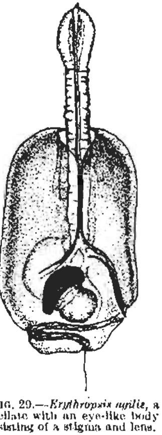

FIG. 29.—*Erythropsis agilis*, a flagellate with an eye-like body consisting of a stigma and lens.

(*After Fauré Frémiet. From F. Doflein, "Lehrbuch der Protozoenkunde," 4 Aufl. Jena, 1916, G. Fischer.*)

Radl (1912) points out features in the structure of the optic organs and centres which are common to the entire animal world. Zawarzin (1913, p. 162) refers to a striking similarity in the structure of the optic ganglia in insects and vertebrates. Certain of the cells (for instance, the bipolar cells of the retina in vertebrates and the outer cells of the first ganglion in insects) are wonderfully similar in shape in both groups. "Such a similarity in the most

[1] According to Zawarzin's terminology.

delicate structure of the highly differentiated optic centres," says Zawarzin (p. 173), "undoubtedly implies, not convergence simply, but a principle of structure connected with the faculty of vision common to the entire animal world."

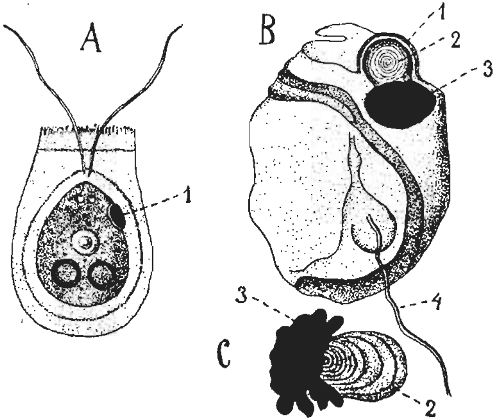

FIG. 30.—*A*, *Eudorina elegans*: 1. Stigma. *B*, *Pouchetia cornuta*: 1. Plastic layer; 2. Lens; 3. Pigment body. *C*. Stigma of *Pouchetia juno*: 2. Lens; 3. Pigment.

(From F. Doflein, "Lehrbuch der Protozoenkunde," 4 Aufl. Jena, 1916, G. Fischer.)

15. Existence within the digestive tract of the host gives rise to a tendency in the parasite towards a *segmentation* of the body. As examples may be taken Cestoda, Catenata (parasitic Peridinea, such as *Haplozoon lineare*), Infusoria (Anoplophrya), Gregarinae (Taeniocystis), Flagellata (*Cyclonympha strobila*). "Taeniocystis and Cyclonympha," says Dogiel (1917, p. 56), "may serve as the best illustration of the principle that similar vital conditions in various animals produce similar and strictly parallel modifications of structure."

16. The projecting chin, as is well known, constitutes one of the distinctive features of *Homo sapiens*. That branch of the Primates which gave origin to man, followed in its evolution the direction towards a prominent chin.[1] *According to the* researches of Klaatsch (1909, p. 113), however, there can be no doubt that the projection named had developed polyphyletically, *i.e.* independently in various races of mankind : the primitive aboriginal forms were entirely destitute of that feature.

17. In the fossil club-mosses are now known certain structures analogous to seeds. Thus, in the small Lower Carboniferous club-moss Miadesmia, recalling Selaginella, has been discovered an organ *resembling* a true seed. Other club-mosses, possessing seed-like reproductive bodies, occur : such is the arborescent Palaeozoic club-moss Lepidocarpon, allied to the Lepidodendrons (see Lotsy, 1909). The contemporary angiosperms, say Arber and Parkin (1907), have undoubtedly been derived from other less developed seed-plants ; but the seed itself, as an organ, and that very highly developed, originated in much earlier geological periods, long before the angiosperms appeared. According to D. H. Scott (1923, p. 59), the seed-plants (=gymno-*sperms + angiosperms) have always been distinct from any* known line of vascular cryptogams, and are not descendants *of these. Thus, seeds of phanerogams and "seeds" of* cryptogams are parallel structures.

Lotsy (ii, 1909) further points out that leaves have arisen in diverse groups of liverworts ; moreover, the spores of these same plants have repeatedly been endowed with the faculty of germination within the sporogonium.

18. Various points of physiological parallelism have been revealed between animals and plants, which are truly remarkable. In certain insectivorous plants, for the digestion of animal food, a ferment similar to pepsin is secreted by corresponding organs (especially in Nepenthes ; see N.

[1] Compare above the researches of Bolck on the gibbon.

Ivanov, 1918, p. 109 ; 1919, pp. 11 *sq.*). Vines (1877, 1887) has established an analogy between the pitchers of Nepenthes and the mucous membrane of the stomach, which likewise contains a zymogen transformed into an active ferment under the influence of acids. The vegetable pepsin of Nepenthes in an acid medium digests albumen (white of the fowl's egg), fibrin and legumin. As a result of digestion peptones are produced. Doubts were expressed as to whether the ferment of Nepenthes is not of a trypsinic character, but Abderhalden and Teruuchi (1906) have demonstrated that the juice of Nepenthes and Drosera do not hydrolyse the peptides, *i.e.* are deprived of the fundamental property characteristic of trypsins. The experiments of G. White have also confirmed the pepsinic character of the ferment of insectivorous plants. "If such is the case," says Ivanov (1918, p. 109 ; 1919, p. 13), "then the occurrence of pepsin in insectivorous plants and the extracellular character of the assimilation of proteins points to a high degree of physiological differentiation, which is only possessed by the higher animals, as the presence of pepsin in invertebrates is still a matter of doubt."

To the same class of phenomena may be referred the circumstance that *cellulose*, that seemingly typical product of the vegetable kingdom, is likewise secreted by tunicates, where it occurs in the test. Dogiel ("Comparative Anatomy of Invertebrates," 1923, p. 69) has further discovered cellulose in the skeleton of the parasitic infusorians, Ophryoscolecidae. According to the researches of Schulze (1922) it appears that *chitin*, so widely distributed in the animal kingdom (Hydrozoa, Bryozoa, Lingula, Annelida, Hirudinea, Mollusca, Arthropoda) is in its chemical structure very similar to cellulose.

We may finally remark that *chlorophyll* and *haemoglobin* are allied substances : it has been established by the investigations of Nencki, Marchlewski and Zaleski that the molecule of both contains a nucleus to a certain degree approximating

these pigments to dye-stuffs of the indigo group. Quite recently Manoilov ("Medical Gazette," 1923, N. 15, Russ.) has discovered a reaction for the discrimination of the blood of man from that of woman; it is remarkable that the same reaction afforded the means of distinguishing the *male* from the *female* sex in dioecious plants: the maple (*Acer negundo*), nettle (*Lychnis dioica*), Vallisneria. (Manoilov, 1923).

Such a physiological parallelism indicates that the elaboration of chemical substances (which ultimately affect morphology, as well as physiology) is subject to certain laws. *In this case there can be no question of infinite variations in all directions.*

Contrivances for the capture of live prey have been evolved in most diverse families of plants: as in sundews (Droseraceae), in bladderworts (Lentibulariaceae), in pitcher-plants (Nepenthaceae) and others; all the families mentioned belong to different orders (the sun-dews to Parietales, the bladderworts to Tubiflorae and the pitcher-plants to Polycarpicae).

19. *Pollination by the aid of insects (entomophily) has* developed independently (convergently) in various groups of plants: in the Cycadeae, Gnetales, angiosperms (Ranales). It was formerly supposed that entomophily had developed from anemophily (fertilization by the aid of wind), but, as has been shown by Diels (1916, p. 769-770), both methods occur in the gymnosperms: they are phylogenetically equivalent in angiosperms.

In the numerous examples that have been offered in this chapter (and their number might easily be multiplied) we have shown that convergence affects the most fundamental organs in animals and plants, that the phenomenon is widely distributed, and that the points of similarity which have been attributed to common descent are often due to convergence.

We have thus *no right to interpret points of similarity* in any organs of any two groups of organisms as being in every case due to common descent, for such similarity may arise, and has actually arisen, not genetically, but in the course of convergence. In studying phenomena of convergence we may trace (as Kant foretold, prompted thereto by an intuition of genius) the laws (or direction) of development, which operate in any given group. In reptiles, for instance, we may note two fundamental stems, one leading towards mammals through Theromorpha, and another towards birds through dinosaurs, pterosaurs and crocodiles. These points of similarity, however, do not attest any genetic connection between the groups named. If we place them not far apart in the system, we thereby only give expression to the idea that the chemical structure of the proteins of their cells possesses similar properties, wherefore the laws of evolution of these organisms are also similar. When the lines of evolution have been traced out for a large number of organic groups, it will be possible to construct a natural system of the animal and vegetable kingdoms—natural, not in the sense of phylogenetic relationship (the determination of the origin of any one group from others will always remain guess-work), but in that of their reciprocal "chemical" affinity. It will then be possible to group organisms together in series and systems, as is done with chemical combinations and crystallographical forms.

Both convergence and homology (similarity due to relationship) are governed by laws. Therefore, if evolution is nomogenesis, chance and natural selection evidently play no part in the origin of new organic forms.

13. PHYLOGENETIC ATAVISM

Phylogenetic atavism (as distinct from individual atavism) may be called the phenomenon which is the reverse of acceleration: it is the manifestation in adults of the features of ancestors.

1. In 1893 the Belgian palaeontologist Dollo asserted that evolution is an irreversible process: organisms cannot revert, even partially, to a condition already passed through in the series of its ancestors. At the same time, and nearly in the same words, this belief was expressed by Gadow (1893, pp. 100-101): "What in the course of ages has phylogenetically disappeared cannot again recur."

In so categorical a form this assertion cannot, of course, be maintained, for, as we now know, characters may be dominant and recessive. Remaining throughout a long period in a latent condition, a recessive character may be manifested again, when a concurrence of certain conditions favourable thereto arises.

If the phenomena of atavism, be they in the form of a reversion to the conditions of more lowly organised forms (as, for instance, in the case of tridigitate feet in the horse, or in that of supernumerary nipples in woman), or in that of an arrest of embryonic development (such as cervical fistula and cleft palate) do not constitute rare occurrences in the lives of individuals, I see no grounds why atavism should not be manifested in the life of a species or genus, etc.

In his work on "Variation in Relation to Age and Evolution" Shitkov (1922) says on this head that "it is probable that the organism, if one might so say, never forgets. It harbours within itself factors of all the characters of the entire line of its ancestors, and in favourable conditions ancient features may either gradually or suddenly be brought to light."

Let us take some examples of reversibility of the processes of evolution, beginning with cases in the life of the individual.

With the fungus *Saprolegnia mixta*, living on dead flies, Klebs supported a continuous growth of the mycelium during six years by placing the organism in optimal conditions of nutrition. Throughout that period of time the organs of reproduction failed to develop. But as soon as the conditions of nutrition were changed for the worse, the

formation of the reproductive cells recommenced. If the fungus be again supplied with food, then at a certain stage "the process assumes a reversed course, and the organ of reproduction, which has commenced to develop, is transformed into a vegetatively growing thallus."

The facts revealed by the doctrine of hybridisation (Mendelism) demonstrate that recessive characters not infrequently appear in organisms in old age. In general, *the tendency of characters to become dominant weakens with age.* By crossing yellow-seed with green-seed peas, Zederbauer (1914) found that the lower flowers, which come first in order, exhibit a more marked dominance of the yellow colouring of the cotyledons over that of the green than do the upper flowers when the plant has grown older. In the hybrids of the stinging nettle, the dominance of a certain character is observed only in young leaves (Correns).

To the same class of phenomena may be referred the appearance in adult (spawning) anadromous salmon (Salmo Oncorhynchus) of the nuptial coloration, recalling that of the young fish (parr).[1] Thus there are no grounds for agreeing with Tschernavin (1921), who connects the phenomenon of nuptial coloration of the Salmonidae with the problem of the origin of anadromous salmon from marine or fresh-water forms.

Hyatt has observed that ammonites in their old age fall, as it were, into second childhood : species with complex septa form simpler ones in their old age. In genera with coiled shells the last whorls are but slightly coiled or may even be uncoiled. Shitkov (1922) has adduced many instances of the manifestation in old age of primitive characters,[2] in man as well as in other animals.

[1] Thus, in young salmon the coloration of the parr type (with dark transverse bands) may be regarded as a manifestation of characters due to phylogenetic acceleration.

[2] Shitkov refers, among others, to the following cases mentioned by Darwin. Black bantam cocks become redder as they advance in age. The cuckoo or blue-mottled Dorking cock, when old, acquires yellow or

Haecker (1922, pp. 19-20) refers to the following cases of reversibility. In the Paguridae (hermit-crabs) the abdomen being, as is generally known, concealed within the shell of a mollusc, grows softer. By removing the protecting shell Przibram (1917) caused the abdomen of that crustacean to resemble the normal abdomen of its free-living congeners : it became hard, flat, distinctly segmented, pigmented and with a definite pattern. In the fly Drosophila a number of cases of return mutations have been observed, as, for instance, the bar-eyed race producing normal-eyed mutants (May, 1917). In the pea a reversion from the form with rose-coloured to that with violet flowers may occur. In feral domestic pigs the colouring and some other characters of their wild congeners have been observed to occur.

Let us now consider some cases of reversibility of evolution in the course of phylogenesis.

In the skull of vertebrates a free quadrate, as is assumed, is the fundamental primordial condition from which the fixed quadrate has been evolved. But it may be presumed that a certain mobility of this bone in some of the dinosaurs is a secondary phenomenon : forms with a fixed quadrate gave rise to forms with a free one (Versluys, 1910, 1912).

In the late glacial or Yoldian time, in the Baltic Sea, which was at that time connected with the White Sea by means of the regions of Ladoga and Onega, occurred a fish, *Myoxocephalus quadricornis*, distinguished, as may be seen from its scientific name, by possessing four bony " horns " or excrescences on its head. When in the Ancylus epoch the Baltic Sea became a fresh-water lake, this bull-head underwent a modification : it was transformed into the form *relictus*, destitute of horns on the head. Remains of this latter form have been found in a fossil state in Sweden, to the north of Lake Mälar, while in Lakes Wetter, Wener and

orange instead of the usual grey hackles. Both in the case of bantams and Dorkings this phenomenon is a reversion to the original form, namely, *Gallus bankiva*, which possesses a red and orange plumage. (See Darwin, " Variation of Animals and Plants," chap. xiii, p. 39.)

Onega it is still living. When in the Littorina epoch the Baltic was again turning salt, and found a communication with the ocean, the form *relictus* reappeared in its original four-horned state. In this latter condition it lives to this day (Berg, 1916, p. 1354).

Analogous modifications have been experienced by the crustaceans *Limnocalanus grimaldii* and *Mysis oculata* in the Baltic Sea (Sv. Ekman, 1913, 1913-14).

Plate (1920, p. 222) adduces the following cases of reversibility of evolution among the West-Slavonian Paludinae. Neumeyr has described a series of *Melanopsis pygmaea*, which commences with smooth shells and reverts again in one of its lateral series to the smooth-shelled *recurrens*. Some of the terminal stages of the Steinheim mollusca of the *Planorbis multiformis* series (of which we have spoken in chap. ii) have reverted to the fundamental types: *Planorbis revertens* and the terminal stages of *Pl. crescens* are exceedingly like *Pl. kleini*; *supremus* corresponds with *tenuis*, etc At the end of their period of development the ammonites again returned to their uncoiled forms.

In a word, it cannot be doubted that evolution may *sometimes* be reversible.

2. Suschkin (1915) has devoted a very interesting article to proving that evolution is reversible. He points out that in penguins (Sphenisciformes), in distinction from all other birds, not excluding Archaeopteryx, the tarso-metatarsus retains throughout life deep fissures between the metatarsalia.

We may take a similar example from the vegetable kingdom. The family of Resedaceae belongs to angiosperms of the order Rhoeadales. This order, in the classification of Kuznetzov, is referred to the lower angiosperms, namely, to the group of Polycarpicae. In the Resedaceae the gynoecium consists of 2-6 carpels, which are either free or united together. In the latter case the *ovary is not fully closed above; it is half closed*, as in the mignonette. As is generally known, the principal

difference between gymnosperms and angiosperms in the *structure of the gynoecium consists in the carpels* of the latter constituting a *closed cavity*, or ovary, which contains the ovules. And in the Resedaceae alone of all *angiosperms we meet with a structure that reverts*, as it were, to the type of gymnosperms.[1] But it is at the same time remarkable that in the Resedaceae occurs a high specialisation in the flower, which in their case is bilaterally symmetrical.

But let us return to the penguins. If we apply to them Dollo's law, says Suschkin, we ought to come to the conclusion that penguins diverged from the general stem of birds before Archeopteryx did so. "Consequently, all the features of similarity between penguins and the remaining birds must have developed parallel to each other or convergently, including the characteristic peculiarities of the *palate, the keeled sternum, and even the skeleton of the* fore-limbs" (pp. 13-14). And yet the giant penguin Cladornis from the Lower Miocene of Patagonia has a normal (fused) tarso-metatarsus. Suschkin presumes, therefore, that the primitive structure of the tarso-metatarsus in penguins is a secondary character, an independent reversion to the ancestral condition. "The traits of the past, which have disappeared from the frame of an adult organisation, may thus again reappear in that of the progeny, emerging as it were *from out of the depths of ontogenesis*. We may say that in any given character the ontogenetic process in the descendants comes prematurely, as it were, to an end, not reaching the concluding chapters, which have been regularly traversed by the ancestors. And the former character returns at the expense of ontogenesis being prematurely broken off" (p. 19).

Referring further to the observation of Sobolev (1914) on the reversion of characters in many Upper Devonian goniatites, Suschkin *concludes that, in admitting the principle of* reversible evolution, "the necessity of explaining nearly all

[1] Kuznetzov, 1914, p. 501.

the points of similarity by means of parallelism in development or convergence is obviated " (p. 29).

It is evident, however, that atavism, or the reversion of characters, is of a very rare and exceptional occurrence. The *whole course of the evolution of the organic world is witness thereto.* True, cases of regression are not infrequent, but regression is something different from atavism. On the other hand, parallelism and convergence, even in the most evident manifestations, may be observed constantly: it is the law of the evolution of all organisms, as we have already shown.

If the point of view of the principle of reversible evolution were consistently carried out, it would be equivalent to admitting that the aboriginal forms were more specialised *than their alleged descendants.* Thus, if it be admitted that the points of resemblance between dinosaurs and birds are not due to convergence, but are the result of the descent of birds from dinosaurs, and if the principle of reversible *evolution be accepted on the widest scale, it would then be* necessary to assume that the tarso-metatarsus in all dinosaurs was constructed after the type of Ornithomimus, but in the course of time reverted in the majority to its former condition, and that all of them possessed an ornithic pelvis, which then reverted to its primitive condition and subsequently assumed the condition which may be observed in Saurischia. In short, it would be necessary to make a series of scarcely probable admissions, which would finally result in our regarding the ancestors as being more specialised than their descendants. It would be a kind of preformation, not potential, as is supposed by some contemporary followers of Mendelism, but actually expressed: such organisms would occur in a fossil state. Such views, however, are opposed by facts from palaeontology. And Suschkin evidently does not share such an extreme view, for he himself admits that the reversion of characters which have been lived through, has its limits, and in very many cases irreversibility may be regarded as the rule (pp. 33-34).

The general aspect of the evolution of the organic world clearly shows that *Dollo's law*, in spite of particular exceptions, *is on the whole true*.

From the foregoing (chaps. ii-iv) it may be seen that the organism represents a complex of characters which in a great measure develop independently: some features progress slowly, or even remain at the same level; others are in advance of their age, and reach a height that will be attained in allied groups only after much time has elapsed. In a word, the rate of the evolution of various characters is not uniform. And, as a consequence, organisms may very often be met with in which are combined features of a very *high organisation with those of a very low one*; *such are* the sharks, dipnoan fishes, Seymouria, seed-"ferns" (Pteridospermae), Bennettitales. This mixture of styles—archaic *and modern—is very widely distributed.*

There are, therefore, no grounds for regarding as a reversion to an ancestral condition every case in which characters of *a low organisation occur in an animal side by side with those* of a high one.

Reversion in development is thus a phenomenon of a particular character, which *has* a *restricted sphere of* application.

However that may be, the principle of reversibility merits the most serious attention in the problem of evolution as determined by law. Reversion, whenever it occurs, even if only in exceptional cases, takes place, as does phylogenetic acceleration, in compliance with definite laws; and there can be no question of a reversion to ancestral characters by chance. But, if the element of chance is eliminated, so **also is the rôle of natural selection.**

All that has been exposed in chapters ii-iv of this work enables us to formulate the following law, which, in our opinion, is very important.

VI. (cf. p. 155). *Both in phylogeny and in ontogeny characters develop at a different rate: some repeat, as it were, the former stages, others predetermine the future ones.* What could not be expressed during the process of ontogeny in some forms, is acquired by others in the process of phylogeny: thus, for instance, vertebrates embody what is indicated in the ontogeny of tunicates. In the process of phylogenetic development organisms produce characters that are a repetition of those present in forms occupying the same, or a much higher, degree of development (sometimes even of such forms as will appear fully developed much later).

The law, thus formulated, is but another expression of the idea that both ontogeny and phylogeny are subject in their course *to the same laws* (cf. Law V on p. 155).

Law VI. leads to the following conclusion:—

VII. *Every organism consists of a combination of characters which evolve to a considerable degree (sometimes entirely) independently one of another.*

Mendelism supplies us with a rule analogous to this law of the inheritance of hereditary units (or groups of units).

CHAPTER V

CONVERGENCE OF EXTERNAL CHARACTERS

> It should not be overlooked that certain strongly marked variations, which no one would rank as mere individual differences, frequently recur owing to a similar organisation being similarly acted on, of which fact numerous instances could be given with our domestic productions.
>
> DARWIN, 'Origin of Species,' chap. iv, p. 72.

WE shall *now pass on to consider* external *characters.* It was with these Darwin was chiefly concerned. Contemporary comparative anatomists and embryologists, however, are not disposed to attribute to them any great importance. Yet *such an opinion is quite erroneous. To begin with,* the difference between internal and external characters is purely conventional. Are teeth, for instance, external or internal characters? Or are gills?

Alluding to the question of convergence (isomorphy) in birds, Gadow, in his fundamental work on that class of vertebrates, expresses himself as follows (1893, p. 64). It is easy to conceive that two groups of birds of a perfectly distinct origin may become so like each other in the structure of many organs *that the sum of similarities* will exceed that of differences. But it would be erroneous, of course, to conclude therefrom that they were closely related. All organs without exception may be subject to adaptation and to *corresponding variations (isomorphy)*: *it cannot be* asserted, although such an opinion is very prevalent among anatomists, that external characters are less constant than the so-called structural or anatomical ones. For some

reason it is claimed that the skeleton belongs to one of the least variable systems of organs. Yet, sometimes a small notch in the beak or some definite primary in the wing is obstinately maintained throughout whole orders of birds. Such is the opinion of Gadow, which we fully share.

In what follows we shall consider the phenomena of convergence and parallelism in so far as they are manifested in external characters and are not affected by the influence of the geographical landscape (*i.e.* in so far as they are due to inner, autonomic causes). We again repeat, that there is no fundamental difference between external and internal characters.

1. CULTIVATED PLANTS AND DOMESTICATED ANIMALS

(*a*) *Vavilov's observations on cultivated plants.* Vavilov studied parallel variations in diverse cultivated plants and was able to state the following very important law, which he calls the law of homologous series of variation (1922, p. 75).

Species ("Linneons") and genera more or less nearly related to each other are characterised by similar series of variation with such a regularity that, knowing a succession of varieties in one genus and species ("Linneon"), one can forecast the existence of similar forms and even of similar genotypical differences in other genera and species ("Linneons"). The similarity is the more complete the more nearly allied the species ("Linneons") and genera are to one another. Whole botanical families in general are characterised by a definite cycle (series) of variability which goes similarly through all genera of the family.

By his observations and experiments Vavilov proved the doctrine of nomogenesis in a more convincing manner than I have been able to do in the present work. Let us borrow some examples from his above-mentioned article.[1]

[1] Compare also Vavilov, 1923.

1. The parallel series of forms in wheats is remarkable. Altogether seven species [1] of cultivated wheats are known to science. Of these *Triticum vulgare* (common wheat) and *Tr. spelta* (spelt) each produces the following forms: (1) bearded and beardless, (2) ears white, red and black, (3) ears hairy and smooth, (4) grains white and red, (5) winter and spring.

The following species—*Tr. durum* (hard), *Tr. turgidum*, *Tr. polonicum* (Polish), *Tr. monococcum*, *Tr. dicoccum* (emmer)—are almost exclusively represented by bearded wheats,[2] but in other respects they produce the same varieties of forms as the preceding species.[3]

As is shown by Flaksberger (1922), the pygmy wheat (*Triticum compactum*) is not a taxonomic unit of equal value with other Triticum species, but there are pygmy forms among different wheats, *i.e.* in the soft wheat (*Tr. vulgare*), in the hard wheat (*Tr. durum*), in *Tr. turgidum*, in Polish wheats (*Tr. polonicum*), in emmers (*Tr. dicoccum*). Among *Tr. monococcum* and *Tr. spelta* pygmy forms are not known as yet.

The same phenomenon of parallelism may be observed in barleys. *Hordeum vulgare* and *H. distichum* each produces the following varieties—(1) ears dense, loose and intermediate, (2) ears black, yellow and red (anthocyanin), (3) empty glumes, hairy and smooth, (4) grains hulled and without hulls, (5) winter and spring, (6) awns smooth and rough.

Further, each of the following representatives of the section Euavena of the genus Avena (oats), *A. sativa* (cultivated oats), *A. fatua* (wild oat-grass, or haver, a weed of flax crops), *A. ludoviciana* and *A. sterilis*, produce varieties

[1] According to Flaksberger, 1923.

[2] In *Tr. dicoccum* and *Tr. polonicum* semi-bearded forms occur too (Flaksberger, 1923, pp. 24, 71).

[3] Parallel series may be observed also in *Aegilops*, a genus allied to Triticum (compare Popova, 1923).

with white, yellow, grey and brown flowering glumes, spring and winter.

Agropyrum repens (couch grass) and *A. cristatum* each form the following varieties (1) ears bearded and beardless, (2) glumes smooth and hairy, (3) ears yellow, red and black, (4) seedlings recumbent and erect, (5) straw thin and thick, (6) leaves narrow and broad, (7) ears dense and loose, (8) ears covered with wax and without wax (9) anthers yellow and violet, (10) stems short and long, (11) leaves hairy and smooth, (12) types hydrophilous and xerophilous, (13) early and late varieties.

2. Thus far parallel series within the limits of one genus have been presented. But the same phenomenon is manifested in different genera of the same family. Thus, Vavilov has detected a pronounced polymorphism in rye (*Secale cereale*), in which is repeated what has been already noted above for wheats (Triticum).

Vavilov was successful in discovering hitherto unknown varieties of rye, similar to wheat, the existence of which he had predicted. Thus, when he found in 1917 among Pamir (Shugnan) wheats several hitherto unknown varieties without a ligula at the base of the leaf-blade, he based an assumption on the principle of homologous variation, and predicted *a priori* the possibility of the occurrence in nature of varieties of rye likewise without a ligula. The year 1918 confirmed his suppositions. Such varieties were found amongst the Pamir (Shugnan) spring ryes (1922, p. 60). Among the same Pamir ryes was also discovered a variety of rye parallel to the already known variety of wheat with hairy ears.

Vavilov, further, points out the following facts. Among the Papilionaceae, in Pisum (pea), Lathyrus (chickling vetch), Ervum (lentil), Vicia (vetch), we find in each genus varieties with white and with anthocyanin flowers, large and small leaves, with the utmost diversity in the colouring of seeds—light, green and all shades ending in black—with

unicoloured and variegated seeds, with greenish-yellow and red cotyledons, normal sized and dwarf varieties, early and late forms. In the family of Cucurbitaceae, among the water-melons (*Citrullus vulgaris*), melons (*Cucumis melo*), cucumbers (*Cucumis sativus*), pumpkins (Cucurbita), varieties with round, oblong and flat, simple as well as segmented fruits are met with; the fruits may be unicoloured, spotted and striped, with the pulp colourless, with coloured plastids or with the juice containing anthocyanin. Melons have usually simple leaves, while water-melons have dissected ones; but some varieties of melon have dissected leaves, and *vice versa*: varieties of water-melon are known which approach ordinary melons in the shape of their leaves. The resemblance between some varieties of melons and water-melons may be so great as to make nearly impossible the determination of the genus. So eminent a botanist as Korschinsky described erroneously a certain variety of melon as being a natural hybrid of *Citrullus vulgaris* and *Cucumis melo* (Vavilov, 1922, p. 63).[1]

Zederbauer (1907) has prepared the following table exhibiting parallel variations in the spruce, larch and pine:—

Variety.	Picea excelsa	Larix europaea	Pinus silvestris
pyramidalis (pyramidal)	×	×	×
pendula (pendulous)	×	×	×
nana (dwarf)	×	×	×
prostrata (prostrate)	×	×	—
virgata (serpentiform)	×	×	×
nudicaulis (twigless)	×	—	—
glauca (leaves with bluish efflorescence)	×	×	×
argentea (leaves silvery)	×	×	×
aurea (leaves golden yellow)	×	—	×
variegata (leaves variegated)	×	—	×

[1] Compare also on parallel series in Cucurbitaceae, Vavilov, 1922[b], pp. 185, 199, 210 (Russ.), and in Cruciferae, Miss Sinskaja, 1923.

3. Series of parallel variations may be observed also in distant families, even in distant orders and classes, both in cultivated and wild forms. Such are the phenomena of albinism, gigantism, nanism, fasciation. The formation of roots, the shape of fruits, the colour of flowers and fruits, etc., undergo similar modifications. In root crops belonging to the most various families, the same types of roots are encountered—oblong, cylindrical, nearly rhombical, spherical, flattened; these forms may be observed in the carrot and celery (both of the family Umbelliferae), the beet (fam. Chenopodiaceae), and the turnip (*Brassica rapa*, fam. Cruciferae). (Vavilov, p. 79.)

(*b*) *Darwin on analogous or parallel variation and Cope on homologous groups or series.* Both in the "Origin of Species" and in "Variation of Animals and Plants" Darwin deals with what he calls "analogous or parallel variation." "By this term," says Darwin ("Variation of Animals and Plants," chap. xxvi, p. 348), "I wish to express that similar characters occasionally make their appearance in the several varieties or races descended from the same species, and more rarely in the offspring of widely distinct species." He takes, among others, the following examples. Smooth peaches, or nectarines, have independently arisen *in various localities* from the pubescent forms; and in this connection it is remarkable that the varieties of peaches and nectarines repeat each other: in both occur kinds with fruit clingstone and freestone, with flesh white, red and yellow, with leaves serrated and without glands, or crenated and furnished with glands, etc.[1] It should be remarked, adds Darwin (chap. xxvi, p. 348), that each variety of the nectarine has not derived its character from a corresponding variety of the peach. Similar parallel forms occur in various kinds of apricots. Some kinds of melons produce fruits which very much resemble those of other genera of the same family of Cucurbitaceae, such as cucumbers, etc. Feather-footed races occur in poultry,

[1] See also "Variation of Animals and Plants," chap. x, p. 342.

pigeons and canaries; in some breeds of the domestic pigeon the wing-bars, instead of being simply black, as in the rock-pigeon, are similar to the bands on the wings of other wild species of the pigeon family, etc. Pug-nosed muzzles occur in pugs and bulldogs.[1]

Hornless cattle have independently arisen in Europe, Africa and South America. Absence of horns occurs in cattle, sheep, the yak and the zebu. Darwin had investigated the domestic pigeons of India: "they are varied in a remarkably similar manner with our European birds" ("Variation of Animals and Plants," chap. xxviii, p. 422). Turnspits (dogs with short and crooked legs) have independently developed in ancient Egypt and Europe (*ibidem*, chap. i, p. 17). Aristotle ("Historia Animalium," ii, 1, 499^b, 12) makes mention of one-hoofed pigs, which are found in Illyria, Peonia and in other places; the same anomaly in pigs has been observed in different parts of the world; "although," says Darwin (*ibid.*, chap. iii, p. 75), "this peculiarity is strongly inherited, it is hardly probable that all the animals with solid hoofs have descended from the same parents: it is more probable that the same peculiarity has reappeared at various times and places."

In this case we are interested only to see in how far the occurrence of such anomalies in various orders of mammals is subject to law. But, along with Osborn, we hold that such single aberrations cannot, beyond the conditions of artificial breeding, give origin to new varieties.

[1] Pug-nosed varieties are also not infrequently met with in fishes, as in the carp, minnow (*Phoxinus phoxinus*), *Vimba vimba* (or *Abramis vimba*, the "Zärthe"), pike, brook trout, salmon, grey mullet (Mugil), eel, cod, etc. This peculiar feature, according to the experiments of Knauthe on *Leucaspius delineatus*, is inherited in accordance with Mendel's law (see Gemmil, pp. 48-50). Short-muzzled varieties are known likewise in the pig (especially in the Yorkshire pig) and in the wolf bred in captivity (a rudimentary short-muzzledness); a kind of short-muzzle may be observed in cattle (type *frontosus*). (See Häcker, 1918, pp. 266-7.)

Osborn (1912, p. 191) submits the following table illustrating identical variations in different mammals:—

	Man.	Horse.	Cattle	Sheep	Stag	Pig.	Dog.	Cat.	Rabbit	Guinea pig	Mouse
Horns in hornless species	×[1]										
Absence of horns in horned species				×							
Appendages to jaws	×			×							
Shortened extremities				×			×				
Multidigitate aberrations	×			×	×	×	×				
Pronounced hirsuteness	×		×	×			×				
Absence of hair		×	×				×				×
Curly hair	×			×							

Häcker (1918, p. 146) has given a table showing the parallel forms of albinism in the domestic mouse, rat, guinea-pig, rabbit, hare, horse, cattle, sheep, goat, llama, pig and dog.

As regards the origin of analogous or parallel variations Darwin distinguishes two cases[2]:—

1. Variations "due to unknown causes having acted on organic beings with nearly the same constitution, and which consequently vary in an analogous manner." To this category belong the above-mentioned cases of smooth peaches, of melons resembling the cucumber, of pigeons with reversed feathers on the head and with feathers on the feet,—characters not possessed by the aboriginal rock-pigeon.[3] Darwin presumes that "no one will doubt that all such analogous variations are due to the several races of the pigeon having inherited from a common parent the same constitution and tendency to variation, when acted on by similar unknown influences."

[1] R. Wood, 1917.

[2] "Origin of Species," pp. 125-126; "Variation of Animals and Plants," chap. xxvi, vol. ii, p. 348.

[3] The rock-pigeon, *Columba livia*, is regarded as the ancestor of the domestic pigeon.

2. Variations "due to the reappearance of characters which were possessed by a more or less remote progenitor." This phenomenon is called by Darwin reversion. For instance, in all the most distinct breeds of pigeons sub-varieties occasionally appear coloured exactly like the parent rock-pigeon, with black wing-bars, white loins, banded tail, etc.

We now know that the phenomena included under the term reversion are for the most part due to the segregation of heterozygous combinations.

The first case, embracing analogous variations in species "inheriting nearly the same constitution from a common parent" ("Origin of Species," p. 132), interpreted in the language of Mendelism, signifies nothing more than an unfolding of some latent factors. It is obvious that in this case natural selection is not able to play any part.

Darwin believed that the "analogous variations" to which he had referred as lying beyond the sphere of the operation of natural selection, are an exceptional and rare phenomenon, and that "characters exclusively due to analogous variation would probably be of an unimportant nature" ("Origin of Species," pp. 126-127), evolution as a rule following the route of accidental variations, from which those happening to be useful are selected.

As was shown above and will be dealt with again below, the phenomenon which Darwin designates by the term "analogous variations" *and which we call convergence is, on the* contrary, a fundamental law of the development of the organic world: "a tendency to vary in similar manner," to repeat Darwin's words, *compels the organism to develop in a* determined direction, which excludes the possibility of infinite variability. Then, as we have shown in chapters ii-iv, convergence affects all the characters of the organism most essential for its existence.

"As all the species of the same genus are supposed to be descended from a common progenitor, it might be expected

that they would *occasionally* [1] vary in an analogous manner," says Darwin ("Origin of Species," p. 126). We think, however, that *variations in the same direction* will always ensue *under definite conditions*.

From the study of Triticum, Agropyrum, Hordeum and others, it may be seen that parallelism is displayed in a number of characters, which manifest themselves in accordance with a certain law. These slight characters are just the very ones which, in Darwin's opinion, are acted upon by natural selection; and yet, as may be clearly seen from the foregoing, and as Darwin admitted, they occur without any intervention on the part of natural selection.

"An inherited tendency to vary in a like manner," of which Darwin speaks, is just what occasions the phenomena *of convergence*. It is *not an exceptional phenomenon*, as *was thought* by Darwin, but a *fundamental law* of the evolution of the organic world. With such a *comprehension of* the process of evolution all need for the hypothesis of natural selection falls to the ground.

Cope (1868; 1887, p. 95) also speaks of "homologous groups or series" among animals. He compares these series with organic combinations—alcohols and their derivatives. Among mammals he gives as instances Marsupialia and Placentalia, among birds Altrices and Praecoces, Pullastrae and Gallinae, Clamatores and Oscines; among Lacertilia—Acrodonta and Iguania, Teidae and Lacertidae; among Anura—the Raniformes and Arcifera; among fishes—Characini and "a group of remaining physostomous fishes." "This phenomena generally relates genera of different zoological regions. Mimetic analogy, on the contrary, relates genera of the same region. . . . I believe such coincidences express merely the developmental type common to many heterologous series of a given zoological region" (p. 96).

Cope further (1887, pp. 96 *seq.*) gives detailed lists of parallel forms in Amphibia, in tortoises (Cryptodira and

[1] The italics are mine.

Pleurodira). in the Old World Agamidae and the American Iguanidae, where are represented the following " homologous series " : —

IGUANIDAE.	AGAMIDAE.
1. *Basiliscus plumifrons* Cope, Costa Rica.	1. *Lophura amboinensis* Schlosser, Amboina.
2. *Iguana tuberculata* Laur., Central and South America.	2. *Physignathus mentager* Günther, Siam.
3. *Crotaphytus wislezeni* B.R.G., from Oregon to North Mexico.	3. *Liolepis belli* Gray, from China to S. India.
4. *Phymaturus palluma* Molina, Chili.	4. *Uromastix spinipes* Dand., Arabia, Crete, Egypt.
5. *Phrynosoma cornutum* Harl., U.S., Northern Mexico.	5. *Moloch horridus* Gray, Australia.

These similarities affect not only external but internal features also.

The same idea of homologous series is laid down at the base of the " dynamic " system of higher plants proposed by Hayata (1921). " I regard," he says, " a natural system as a dynamic one, changing with the view of the systematiser and subject to alteration, according to the way in which it is considered, and I believe that none of the species, genera or families has a fixed natural position, but has changeable positions, subject to alteration according to the criterion for comparison."

As proofs of his views Hayata shows that the Orchidaceae, for instance, usually united with Burmanniaceae in the order Microspermae, show relationships with Musaceae, Zingiberaceae, Marantaceae, Triuridaceae, Iridaceae, Amaryllidaceae, Bromeliaceae, Taccaceae, Hydrocharitaceae, Cannaceae, Philydraceae; Betulaceae are connected with Salicaceae, Fagaceae, Juglandaceae, Casuarinaceae, Myricaceae, Ericaceae, Urticaceae. Salicaceae, the single family in the order Salicales, are closely related to the Batidaceae (Batidales) in having a dimerous

> *gynoecium, and also to the Myricaceae and Juglandaceae* in having nearly naked or apetalous flowers. But, on the other hand, the close relationship of the Salicaceae and Tamaricaceae (which stand far apart from one another in the present system) is incontestable: the gynoecium, placentas, ovules, fruits and seeds, or even anatomical characters such as the perforation of vessels, are very much the same in both families. If the presence or absence of sepals and petals is to be credited with a superior value in classification, then the Salicaceae should be brought near the Myricaceae, Juglandaceae or some such group. But, on the other hand, if we attach importance to the structure of the ovary, ovules, fruits, seeds or anatomical characters, then the Salicaceae should find their place near the Tamaricaceae of the Parietales (Hayata, p. 108).

We shall now consider some cases of the convergence (or "analogous variations") of external characters.

2. INFUSORIA, INSECTS, MOLLUSCA, FISHES, BIRDS, ETC.

In the stomach and intestine of ruminants are found in multitudes singular Infusoria of the family Ophryoscolecidae. According to the researches of Dogiel (1923) different species of these Infusoria, belonging to separate genera (Entodinium, Diplodinium, Metadinium, Ophryoscolex), exhibit parallel types of variation: in all genera species are met with and without spines, with one dorsal spine, with one ventral spine, or with 2, 3, 4, 5 or 6 spines, spines large and small; lastly, the shape of the nucleus is likewise subject to similar parallel variations. Even if in certain genera corresponding species have not yet been met with, they will undoubtedly be discovered later on.

Wittenberg (1923) has arranged the genera of Trematoda belonging to the Cyclocoeliidae in homologous series, which have enabled him to foretell the occurrence of certain forms that have since been actually described.

Caddis-flies (Trichoptera) of the genus Dinarthrum fall into four sub-genera, in each of which the development of characters follows parallel lines (Martynov, 1913, p. 78; 1915, p. 434). Two genera of caddis-flies, Apatania and Apatelia, contain such similar species, that an authority on that branch of insects, MacLachlan, placed them in a distinct genus Apatidea. And yet, according to the researches of Martynov (1918, p. 57), the Turkestan *Apatidea elongata* belongs to the genus Apatania, and the Turkestan *Apatidea copiosa* to the genus Apatelia. It is quite possible to indicate in each of the genera the species which are most allied to the species of the former genus "Apatidea": *Apatania elongata* has diverged from *Apatania bulbosa*, and *Apatelia copiosa*, apparently, from *Apatelia mongolica*. But in both cases evolution has followed parallel lines.

The species of bumble-bees (Bombus) vary exceedingly, and at the same time variation follows parallel lines in different species: nearly every species possesses light and dark varieties; in many species with a white end to the abdomen occur forms with a red one.

Identical types of aberration are very common in many insects: as regards coloration, for instance, in beetles of the genera Anisoplia and Cicindela: as regards the length of the wings in bugs (forma *macroptera* and forma *brachyptera*), etc.

Different genera of land Mollusca of the group Helices, although belonging to separate families, exhibit parallel variations in the form of the shell (Pilsbry, p. vii).

Family.	Genus.	Species.		
		Shell *globose*.	Shell *depressed*.	Shell *keeled*.
Helicidae	Helix	pomatia	vermiculata	gualteriana
Eulotidae	Epiphragmophora	californiensis	mormonum	circumcarinata
"	Eulota	acustae	euhadra	plectotropis
Camaeidae	Pleurodonta	nux-denticulata	isomeria	caracolus
Polygyridae	Polygyra	" mesodon "	tridentata	obstricta

The list, says Pilsbry (p. viii), is capable of indefinite extension. Even those minor groups called "sections" often show the same series of changes in forms, thus :

Sections.	Shell *globose*.	Shell *depressed*.	Shell *lens-shaped*.
"Dentellaria"	nux-denticulata	dentiens	lychnuchus
Theldomus	emarginata	petitiana	lima
Pleurodonte	bronni	anomala	peracutissima
Stenotrema	stenotrema	monodon	spinosa
Axina	montfortiana	magister	siquijorensis

The same holds good of the sculpture of the shell : in various genera species with granulate, spirally striate, ribbed, hairy, or smooth shells are met with.

The North American land Mollusca (Helicoidei) externally very much resemble the European forms, and have been until recently described as species of the same genera. But they are anatomically quite distinct, and have therefore been separated into distinct families. The European snail *Helicigona* (*Isognomostoma*) *personata* Drap., of the family Helicidae, in outward form is very much like the American Polygyra (Triodopsis), which belong to another family, Polygyridae (Pilsbry, p. 309).[1] The European *Helicigona* (*Arianta*) *arbustorum* (L.) is very similar to the American Epiphragmophora, which belong to another though allied family Eulotidae.[1]

A series of such similarities between mollusca belonging to various families and different localities has been pointed out by Mrs. M. Linden (1898). Among the Melaniidae occur genera resembling one another in the form, coloration and sculpture of the shell, (1) the turriform shells of Terebra, Pyramidella and Cerithinum, (2) the broad and flat shells of Ampullaria, Paludina, Neritina, (3) the shells of medium height of Achatina. It is remarkable that the shells of Melaniidae, which have the form of the Terebra shell, usually exhibit the sculpture of the latter.

[1] According to Pilsbry, to another group ; but now these groups are regarded as separate families. Eulotidae occur in Eastern Asia and Western America ; in Europe only one species, *Eulota fruticum*, is found. Anatomically Eulotidae differ very much from Helicidae.

Coloration in the shape of dark transverse parallel bars occurs in representatives of various families of fishes (Characinidae, Salmonidae, Cobitidae).

In the most diverse genera of the Cyprinidae appear forms with broad and narrow bodies, as in the bleak, the roach, the dace, and in many others.

Males and females of many fishes are differently coloured. In several species of marine fishes, belonging to various families, red and reddish-brown tints predominate in the females, and in the males blue (sometimes blended with green). These particulars may be observed in the Australian *Ostracion ornatum* of the Plectognathi, in *Hexagrammus decagrammus* of the family Hexagrammidae, which is common on the coast of California, and in the European *Labrus mixtus* of the Labridae. We here encounter a parallelism in sexual *dimorphism*.

In the Cyprinidae two genera, Phoxinus (minnows) and Paraphoxinus have both diverged, the first from the genus Leuciscus (which includes the chub, dace, etc.), the second from that of Rutilus; the representatives of both genera present the same features, being distinguished by small size, small scales, which are often not imbricated, short fins, a backward position of the dorsal fin, and by a peculiar coloration.[1] The Dalmatian *Paraphoxinus adspersus* is wonderfully like *Phoxinus percnurus* in general appearance, but especially in the colouring, which consists of small, dark, sharply circumscribed spots. In no other Cyprinidae has such a coloration been observed.

According to the investigations of Heincke (1898, p. lxix), sprats (*Spratella sprattus*) break up into the same races as do herrings (*Clupea harengus*).

In the fresh waters of Africa and of South and Central America are distributed numerous fishes of the group of families Characinoidei, related to the Cyprinidae. Many genera of Characinoidei closely resemble representatives

[1] See Berg, 1912, pp. 82-3.

of other families. Thus the African Hydrocyon, in the form of the body and in colouring, recalls the white-fish (Coregonus, of the Salmonidae). Some species of the African genus Alestes very much resemble the bleaks (Alburnus, of the Cyprinidae) in the form of the body and mouth, in the elongation of the anal fin and in coloration. *Citharinus citharus*, very common in the Nile, as regards the shape of its body and fins is a true bream (Abramis). Some of the South American Characinoidei (such as Elopomorphus) are like fresh-water herrings (Alosa), others (Salminus) like salmon, yet others (Prochilodus) like grey mullets (Mullus), and still others like darters (small North American Percidae); *Gasteropelecus maculatus* is a flying characin: *Nannostomus unifasciatus*, a cyprinodont-like one. In both groups, Characinoidei and Cyprinidae, the character of variation is the same: it refers in both to the shape of the body, the position of the mouth, the length and shape of the fins, the position of the dorsal fin, the number of gill-rakers, the lateral line being complete or incomplete, the position of the keel on the abdomen, etc.

In diverse genera of the Characinoidei, which have nothing in common, similar features are developed, such, for instance, as a pair of conical teeth in the lower jaw in the African Alestes and South American Brycon; or the elaboration of a three-fold series of teeth in the upper jaw from a double one, or of a double series from a single one, which has taken place independently in various groups (Eigenmann, 1912, p. 109).

Terentjev (1923) studied parallelism in Amphibia, and found that nearly every Palaearctic species of the genus Rana has its long-legged and short-legged sub-species. It is very suggestive that perfectly analogous groups may be likewise established for other families, as, for instance, Cystignathidae and Bufonidae (Terentjev).

In the Falconidae many cases of parallel development may be noted. Thus a general parallelism is manifested

between Herpetotheres (sub-family Herpetotherinae) and the sub-families Falconinae; Poliohieracinae, and, further, between Micrastur (sub-family Herpetotherinae) and the sub-family Polyborinae (Suschkin, 1902, p. 388).

In the sub-family Falconinae may be noted the disappearance of the projection in the superior margin of the prefrontal, and an elongation of the outer margin of the latter in the kestrel (Tinnunculus) and in the hobby (*Hypotriorchis subbuteo*). Among external features may be mentioned a similar coloration of the rectrices in the adult males of the common merlin (*Aesalon aesalon*) and in several species of the kestrel; a uniform slaty coloration of the plumage in the old males of the hobby, *Hypotriorchis concolor*, and in both species of the red-footed falcon, *Erythropus vespertinus* and *E. amurensis*; transverse stripes in various genetic branches of the true falcons (Falconinae), *i.e.* in the kestrel, red-footed falcons, Indo-Ethiopian group of merlins, gerfalcons (*Hierofalco gyrfalco*, *H. islandus*) and the peregrine falcon (*Falco peregrinus*). Single individuals of the saker (*Gennaia sacer*), throughout the entire region of its distribution, show a tendency towards the appearance in the adults of transverse bars on the rectrices and the upper parts of the body, *i.e.* towards variation in the direction of the gerfalcon and the peregrine falcon, which latter are more differentiated forms (Suschkin, 1902, p. 389).

Miss E. Sinskaja (1923) studied parallelism of forms in some cultivated plants of the family Cruciferae, namely, in *Eruca sativa*, *Brassica napus*, *Br. campestris*, *Br. juncea*, *Br. nigra*, *Sinapis arvensis*. She found among them many parallel forms.

> Parallel variations of the following characters are observed in nearly all studied species:—length of the stem, shape of the petals, presence of anthocyanin in the fruit, degree of declination of the siliqua from the stem, differences in the green coloration of the seedlings, size of the seeds, albinism, anthocyanin of the stem, shape of the leaf, colour of the leaves, length of the beak of the

fruit, coloration of seeds, etc. Further, Miss Sinskaja gives lists of species of the family Cruciferae, both cultivated and wild, among which there exist forms (1) with glabrous or nearly glabrous fruits and with pubescent ones, (2) with whole-margined or feebly dentated leaves, with lobate, strongly dentate or emarginate and with pinnate ones, (3) with glabrous and with pubescent leaves, (4) with long and with short fruits, (5) with dwarf and with giant forms, (6) with small and with large ones, (7) with white flowers, with pink, with blue or violet ones, (8) with white or pale yellow flowers and with bright yellow ones. Let us take a single example. Twenty-five genera possess species with glabrous or nearly glabrous fruits and with pubescent ones ; among them are Brassica, Cardamine, Draba, Hesperis, Isatis, Lepidium, Sinapis, Sisymbrium, etc.

Sympetaly has developed independently in both dicotyledonous and monocotyledonous plants. Parallel variations are observed in cypresses and junipers (Zederbauer, 1907).

The fungi Gastromycetes fall into two groups, Plectobasidiineae and Gastromycetineae. Each of these groups in its turn diverges into four divisions, and in these a parallel development in both groups may be observed (Lotsy, i, 1907, pp. 718-9, 727-8).

According to the researches of K. Meyer (1916, pp. 166-167), the liverworts, Marchantiaceae, have developed in two parallel lines : the highest representatives in each line acquired a similar structure, although attained in different ways. The two series are as follows :—(1) Fimbriaria, Cryptomitrium, Priessia, Marchantia, (2) Plagiochasma, Reboulia, Grimaldia, Fegatella.

R. Wettstein (1900) drew attention to *seasonal dimorphism* in Euphrasia. Two well-distinguished species, *Eu. stricta* and *Eu. brevipila*, occur ; each forms a spring, early-flowering variety ; the first produces *Eu. suecica*, the second *Eu. tenuis* ; the seasonal forms, like the maternal, may be easily distinguished one from another. But it is to be noted that *Eu. tenuis* forms a smooth race (*glabra*), which is indis-

tinguishable from *Eu. suecica*. This constitutes an excellent example of parallelism, development in a determined direction and polytopical formation of varieties.

In the foregoing (§§ 1, 2) only a few examples have been offered. They could easily be increased many times, as the whole field of taxonomic biology is full of parallel varieties of the kind.

Some of the varieties named above grow in the same localities; for instance, both wheat and rye without a ligula occur in the Pamir. Geographical conditions, however, apparently do not as a rule exert any influence on the formation of such varieties. For this reason we attribute these and similar cases to the effect of internal causes.

3. FOSSILS

In a very important work referring to the ammonites of the Volga formation, intermediate between the Jurassic and Cretaceous, Michalski (1890) points to a "quite peculiar type of variations consisting in the manifestation and parallel development of certain similar characters in a number of ammonites, which have been produced independently of their genetic affinities" (p. 337). As a result, it sometimes becomes difficult to recognise species of different genera.

Nor is that all. In genetically distant genera may be observed not only similar characters, but *one direction in which subsequent variation follows*. Thus, both Olcostephanus and Perisphinctes develop in a determined direction (p. 165, 437):

> The "strictly determined direction" of variation, observed by Michalski (p. 467), consists in the following.
>
> In genetically distinct groups of ammonites from the Lower Volga beds a peculiar sculpture of the shell is exhibited, which Michalski calls sculpture of the type of *Olcostephanus pallasi*. It is distinguished by multipartite

and closely set ribs being gradually replaced in the direction of adult convolutions by conspicuously raised ribs set at some distance from one another, the latter being at first of a bipartite, and, somewhat later, of a solitary, character (Table iv, Figs. 1-5: *O. pallasi*; Table ix, Figs. 1-5: *P. apertus*). Such a structure is shown in *O. pallasi*, *O. acuticostatus*, *P. apertus* and *P. pavlovi*, the parallelism between which, however, is not confined to the above-mentioned character, but affects also the shape of the transverse section, diminution in growth, etc. But this is not all; the structure peculiar to *O. pallasi* is observed in a series of Olcostephanus from the Neocomian, perceptibly distant from one another, in consequence of which *O. nodocinctus* from the Neocomian, for instance, very much recalls some forms of *O. acuticostatus* from the Lower Volga beds (p. 487).

The following curious fact is also well worth noticing. The Portlandian *Perisphinctes biplex* Loriol (from France), having the outward appearance of *O. pallasi*, approaches three different ammonites from the Lower Volga beds, namely, the extreme variations of *O. pallasi* and *P. pavlovi* and the initial variations of *O. acuticostatus* (Michalski, pp. 486-487, 304-305).

To the phenomena of parallelism in ammonites attention was even earlier directed by Waagen and Neumayr. The former (1869, p. 235) observed that two genera Appelia ("series *Ammonites subradiatus*") and Oecotraustes ("series *Ammonites genicularis*") form parallel species in the same horizons. Neumayr (1889, pp. 111-112), while denying the possibility of an irregular variation, spreading in all directions, points out (p. 113) that in various groups of ammonites of the family Aegoceratidae, for instance, the same types of structure of the shell are manifested, and each type of structure is usually likewise characterised by a similar development of the septa; owing to such analogous variations the determination of species is sometimes rendered very difficult. Thus, parallel series of variations are exhibited by (1) Sehlotheimia, Parkinsonia, Reineckia and certain Hoplites, and (2) group of *Aegoceras henleyi*, Cosmoceras, certain Hoplites, Acanthoceras.

The same phenomenon is further displayed by ammonites of various families, such as Arietites, Harpoceras, Cardioceras, Schloenbachia.

All the foregoing, says Neumayr (p. 114), may be explained solely by the fact that the structure and constitution of the animals enables them to vary only in a limited number of directions; the same characters appear again and again "owing to mechanical influences."

Neumayr further mentions a case of a specimen of an ammonite of the genus Arietites (family Harpoceratidae),

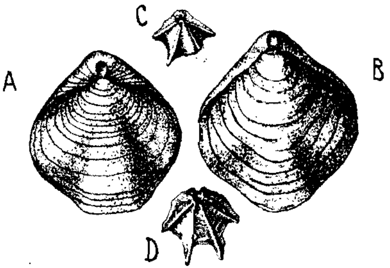

FIG. 31.—*Parallel series in brachiopods.*

A, *Athyris subtilita*, fam. Spiriferidae, Upper Carboniferous of North America. *B*, *Terebratula subsella*, fam. Terebratulidae, Upper Jurassic of France. *C*, *Plicigera trigonella*, fam. Spiriferidae, Middle Triassic of Italy. *D*, *Trigonella fleuriausa*, fam. Terebratulidae, Upper Jurassic of Hanover. (From O. Abel, "Lehrbuch der Paläozoologie." Jena, 1920, G. Fischer.)

which at first developed normally, but subsequently, owing probably to a mechanical injury, began to acquire in sculpture and in the transverse section of the shell the characters of Aegoceras, of the family Aegoceratidae, and that to such an extent that no palaeontologist would hesitate in referring the remnant of that portion of the Arietites to the genus Aegoceras, and even to one definite species of that genus.

Similarly, among brachiopods we meet in Waldheimia with the same types of variation as in Terebratula. Some Upper Jurassic Terebratulidae repeat Carboniferous and Triassic Spiriferidae (Abel, *1920*, p. *240*) (Fig. *31*).

In the family Dreissenidae (of the Lamellibranchiata) shells with wing-like expansions occur in many groups, *i.e.* in

Congeria, both in the "mytiliformes" and the "modioliformes" groups, and in the genus Dreissena (Andrussow, 1897, p. 594).

Abel (1920, pp. 52-53) points out that in various Foraminifera of the nodosarian type the terminal chambers of the shell are constructed after the nodosarian pattern, while the initial chambers are very diverse and correspond to types found in other Foraminifera in the adult condition. It would seem that the nodosarian type has thus been independently obtained from various ancestors at least eight times. Similarly, the type "Textularia" has independently arisen thrice.

The phenomena of parallelism, widely developed in Goniatites, have been fully investigated by Sobolev (1914). By the Lamarckian term *gradations* he means "every intermediate phase assumed by the varying character which develops in a determined direction, if such a phase differs but little from the preceding and following ones" (p. 9). The gradations of Sobolev are nothing but the mutations of Waagen.[1] To gradational variations in Goniatites are subject the size of the shell, the degree of its coiling, the character of its sculpture, and especially of the complexity of the sutural line. Gradational variations in different lines and groups of lines (of Goniatites) often occur in the same order: varying characters in one line assume the same gradation and stages as in another. With such a parallelism in development a series of "species" of some "genus" may experience the same and similarly directed variations, and may thus acquire the characters of another "genus" (pp. 10-11)

In Goniatites parallelism is of exactly the same type as that exhibited in Gramineae (see above, the observation of Vavilov). Therefore, Sobolev very justly remarks that the entire distribution of Goniatites according to genera should be reconsidered, as different varieties not closely related to one another may exhibit similar characters owing to their having developed in the same direction; this would impart

[1] See Sobolev, p. 79.

to different forms a similar aspect, and would thus lead to the grouping together of forms which are, in fact, unrelated.

Neumayr, a convinced adherent of the theory of selection, referring to cases of parallel variations, says (1889, p. 116), "The question arises, whether these causes alone are not potent enough to fix permanently a new character, without the intervention of natural selection. We cannot see any rational grounds why this should not actually be the case, and such a presumption must be considered as a very probable one." But he adds at once, "This, of course, may be true only of such characters as are of no importance to the organism, for, had they been useful or injurious, natural selection would have favoured or prevented their being permanently fixed." But from the examples we have given above (*chap. iv*) *of the development of the osseous, nervous* and circulatory systems, we may infer that the most vital parts of the organism develop in a determined direction.

4. *PARALLELISM IN HETEROGENEOUS VARIATIONS (MUTATIONS) AND ANOMALIES*

We have already referred to this subject when dealing with anomalies in mammals. Gates (1921, p. 44) gives the following table of parallel mutations in Oenothera :—

	lata.	gigas.	semigigas.	nanella.	semialta.	debilis.	cruciata.	elliptica.	virescens.
Oe. lamarckiana - -	×	×	×	×	—	—	—	×	×
,, biennis - - -	×	—	×	×	—	—	×	—	×
,, grandiflora - -	—	×	×	×	—	—	—	—	—
,, stenomeres - -	—	×	—	×	—	—	—	—	—
,, pratincola - - -	—	×	—	—	—	—	—	—	—
,, reynoldsi - - -	—	?	—	—	×	×	—	—	—
,, suaveolens - -	×	—	—	—	—	—	—	—	—
,, multiflora - - -	—	—	—	—	—	—	—	—	×
,, grandiflora × biennis, F_2 and F_3 - -	×	—	?	×	—	—	—	?	—

In various species of the fruit-fly Drosophila the same mutations were discovered by Hyde (1915), Sturtevant (1915), and Metz (1915, 1916).

In *Capsella bursa pastoris*, in various species of the genera Camelina, Veronica, Lactuca, Jurinea, Serratula, and in other plants of our flora, forms with entire and lobate or divided leaves are met with. Zinger (1909, p. 70) draws attention to the fact that both forms often occur in the same environment, and that there are no grounds for regarding one form as being more adapted than the other. There is no ground, he says, for supposing that these forms had arisen through a gradual accumulation by means of natural selection of small individual variations in the marginal dentation of the leaf. Zinger considers the phenomenon referred to as a case of heterogenesis, or mutation.

It is known that features characterising species, genera, or, sometimes, higher taxonomic divisions, often appear in isolated individuals in the shape of anomalies (monstrosities). In the poppy the corolla is choripetalous, but de Vries (1906, p. 405) had in his botanical garden a sympetalous anomaly of *Papaver bracteatum* brought from France. Such an anomaly is very inconstant, as the same stem sometimes carries flowers with both choripetalous and sympetalous corollas. In referring to this case de Vries mentions that genera with a choripetalous corolla sometimes occur as cases of atavism among heaths (Ericaceae), belonging to the lowest representatives of the Sympetalae, such as Ledum, Pirola and others, while choripetalous flowers are sometimes observed to occur, as anomalies, among rhododendrons. De Vries suggests that the Ericaceae have arisen from Choripetalae, and in the same manner as the choripetalous poppy has given origin to its sympetalous anomaly.

Sympetalous anomalies have also been observed in the soapwort, *Saponaria officinalis;* in the traveller's-joy, *Clematis vitalba;* in the campion, *Silene annulata,* etc. De Vries mentions (1906, p. 406 *sq.*) other cases of parallel

anomalies. In various genera possessing pinnate or divided leaves, specimens with entire leaves appear, such as in the blackberry (*Rubus caesius*), strawberry, Aralia, jessamine, locust (*Robinia pseudacacia*), walnut, ash, etc. And, conversely, Korschinsky (1899) describes a series of heterogeneous variations (mutations) with divided, palmate or strongly dentate leaves, namely, in the case of the oak, elm (*Ulmus pedunculata*), alder (*Alnus glutinosa*), lime (*Tilia europaea*), maple (*Acer platanoides*), walnut (*Juglans regia*) and others.

5. INTELLECTUAL SPHERE

Psychical phenomena are likewise subject to convergence.

1. In the case of spiders and swallows W. A. Wagner has found that, for an understanding of the nature of instincts, the "happy thoughts" or "accidental guess-work," such as are alleged to have illuminated the ancestors of our contemporary fauna, are not required ("Comparative Psychology," i, p. 338).

"The designs of the constructions of spiders in general, of their nests and cocoons, do not represent anything elaborated by the species at its own risk and according to its own definite plan; consequently it would be wrong to believe that the constructions of various species of spiders, standing far apart in the system, possess similar designs, and that those of representatives of one and the same genus, perfectly distinct designs" (p. 307). It is not difficult, on the contrary, to show that, as a rule, the structures of spiders are similar in allied groups, and very distinct in genera far apart.

"The peculiarities of the industry of spiders," says Wagner (p. 307; 1894, pp. 261-2), "do not exhibit anything like chance." I am at a loss how to reconcile this very just observation on the origin of instincts in spiders with what the author states in the following page of his book: "Complex instincts, just like morphological characters in animals, may be evolved by means of natural selection through a

slow accumulation of numerous, minute and useful modifications." *When chance is excluded, when every new character, bodily or mental, manifests itself in compliance with law, there is no place for natural selection as an agency in evolution.*

I cannot miss this opportunity of observing that, as has been very justly stated by Wagner, instincts have not been derived from intelligence, nor has the latter been evolved from the former: both have been independently derived, it may be assumed, from reflexes, and have then proceeded to develop *on parallel lines.*

2. As with organisms, so is the development of languages due to phonetic laws. The sounds in language are subject to various modifications, but no one would dream of affirming that the number of such modifications is infinite, and that only such variations are preserved as, let us say, conduce best to ensure reciprocal understanding. The case is actually quite different. Had no other agencies interfered, says Meillet, it would be possible, by knowing the phonetic laws alone, to derive from a given condition of the language its state in any ensuing moment.

The compliance of the development of languages with definite laws is attested, among other things, by each group of the Indo-European languages evolving, after having separated from the aboriginal ancestral tongue, new forms, which are parallel to one another. The common features in the structure of the contemporary Indo-European languages *are in a greater measure due to independent parallel development*, than to the preservation of the aboriginal Indo-European type of language.[1] Thus, in many Indo-European languages a complex past tense has been formed which consists of the participle and the auxiliary verb.

3. Convergence may also affect the value of ideas. A number of cases are known of the independent occurrence of the same manifestations of spiritual and material culture

[1] Meillet, p. 358 (Russian translation).

among various races of mankind, both of the Old and New World. This subject was dealt with by A. Humboldt (1808) and E. B. Tylor (1866) in their time, and later called forth the detailed, but not very perspicuous, disquisitions of the German ethnographer, A. Bastian (1865, 1881). At the basis of such psychical convergencies lie identical or similar elementary ideas (Elementargedanken) inherent in the same form in all peoples, and necessarily produced through internal causes by the same psychical organisation of the whole of mankind.[1] Thus, the fundamental types of implements and weapons are the same in all peoples; in illustration of which may be mentioned bows and arrows, contrivances for procuring fire, wrought stones used as implements and arms, fish-hooks and nets, etc. All such objects have been quite independently invented in all corners of the earth.

Elementary ideas, like organisms, continue to develop under the influence of the environment.

An independent origin can, of course, be attributed in savage peoples solely to elementary ideas, similar to those mentioned above: in more complex cases imitation is to be supposed.

Let us take a few examples of independent coincidences. A "*meandering*" *ornament occurs both in monuments of* classical antiquity and in those from South America. Bronze as an alloy was independently invented in Europe and America. A certain resemblance may be perceived in the architecture of the ancient Egyptians and the ancient Mexicans (Eisenstädter, p. 27). The veneration of ancestors and belief in spirit is spread over the whole world. Various systems of numeration—the binary (Australia, South America), quinary, decimal, duodecimal, vigesimal, have independently arisen among various peoples (*l.c.* p. 152 *seq.*). In the realm of science may be mentioned the perfectly unequivocal statement by Aristotle of the fundamental

[1] See on this subject Eisenstädter, 1912.

principles of the doctrine of the struggle for existence, which was independently arrived at by Darwin.[1] The independent discovery by Newton and Leibnitz of the infinitesimal calculus has also been adduced as an example.

The inference this chapter may help us to make is as follows: the external features of organisms are an embodiment of an accordance with certain laws; these features do not arise by chance; and where chance is eliminated, there can be no scope for the intervention of natural selection in the production of new forms.

Species which have been carefully studied from a systematic point of view, such as cultivated cereals, exhibit a number of minutely differing hereditary forms. These were the forms Darwin dealt with, and the study of which gave the impetus towards the establishment of the theory of natural selection. We must remember that the first chapter of the "Origin of Species" bears the title of "Variation under Domestication." Yet we have seen that all these slightly differing forms arise in various species strictly according to law, without any intervention on the part of chance and hence of natural selection. Much may be said for the supposition that in cases similar to those of parallel series in cereals, Cruciferae, Leguminosae, we meet with an unfolding of a complex of pre-existing characters.

Many of these minutely differing forms are variously affected by physiological agents; thus some varieties of wheats, barleys, oats are subject to rust (Puccinia) and mildew (Erysiphe), whereas others are immune from these pests.[2] Similar cases are mentioned by Darwin ("Origin of Species," chap. iv, pp. 66-67; "Variation of Animals and Plants," chap. xxi, pp. 227-233): "In the United States purple plums suffer far more from a certain disease than yellow plums; whereas another disease attacks yellow-fleshed peaches far

[1] See L. Berg, "Theories of Evolution," 1922 (Russ.).
[2] See Vavilov, 1919, pp. 231-232.

more than those with other coloured flesh; the silk-worms which produce white cocoons resist the deadly fungus better than those producing yellow cocoons." Consequently, natural selection may effect (and has actually done so) the geographical distribution of the above-mentioned forms. But there are no grounds for assuming that it can in any degree, however slight, conduce to the formation of favoured varieties, as these latter were already in existence before it assumed its sway.

CHAPTER VI

THE GEOGRAPHICAL LANDSCAPE AS AN AGENCY IN THE PRODUCTION OF ORGANIC FORMS

. . . öffnet den freien
Blick ins weite Feld der Natur.
GOETHE, "Metamorphose der Thiere."

IN the process of evolution every organism is subject, as we have said, to two kinds of influences. One kind, autonomic, are inherent in the organism; the other influences are derived from the external environment in its widest sense, or from the surrounding living and inorganic medium—in a word, from the *geographical landscape*. These external influences we shall designate by the term *choronomic* (from the Greek word *choros*, signifying place, region), or they may be called *geographical* in the narrow meaning of the word. By "natural, geographical landscape" we understand "a region in which the character of the relief, climate, vegetation and soils are united in one harmonious whole, which is typical of a certain zone of the earth, recurring throughout its entire area" (Berg, 1915, p. 471). Geographical landscapes combine in constituting landscape zones, as examples of which may be regarded the zone of tundras, the forest zone of the temperate climate, the steppe zone, the zone of deserts; as other examples may be adduced the alpine zone in mountains, the abyssal zone of the ocean, the pelagic zone, etc. The landscape does not affect organisms by any one of its component agencies, such as by its altitude above the sea-level, its temperature, or the rocks

forming its soil, but by the entire combination of all the elements which constitute any given landscape.

The geographical landscape affects organisms in *an imperative manner*, compelling all the individuals, so far as the organisation of the species permits, to vary in a determined manner. There is no place here for chance: consequences follow with the same fatal constancy as chemical reactions or physical phenomena. With identical or similar geographical conditions, identical or similar results are bound to follow. All cave animals manifest a tendency towards the loss of colour, a reduction of the eyes, an acquisition of lengthened appendages to serve as tactile organs, etc. Similar modifications, dependent on a certain similarity of the geographical landscape, are experienced by forms inhabiting the depths of fresh-water lakes, as, for instance, by the crustaceans (Gammaridae) of Lake Baikal, as has been pointed out by W. Sowinski (1915). The tundra, the forest, the steppe, the desert, mountains, aquatic environment, life in islands, in the depths of lakes and seas, each of these stamps its mark on organisms. Species that are unable to adapt themselves are obliged to emigrate into other geographical landscapes or to perish.

We shall now submit a few examples of the effects of the landscape upon organisms.

1. FISHES

In studying the fresh-water fishes of Europe, I turned my attention to the following curious circumstance. As we move further south the number of species and varieties of fishes, as of other animals, increases. But, at the same time, it becomes evident that variations in genera very widely separated often exhibit a tendency to develop *in one direction*. Thus, in the South European and Caucasian species of Chondrostoma (of the Cyprinidae) we observe a decrease in the number of the rays of the dorsal and anal fins as

compared with what occurs in the North European and Russian representatives of that genus: in the North European *Chondrostoma nasus* the dorsal fin usually contains 9 branched rays, and the anal 10-11; in the numerous South European species of the same group there are generally 8-9 branched rays in the dorsal fin, while the number of those rays in the anal falls to 9. Such a decrease in the number of rays is still more pronounced in the South European and Caucasian species, which are grouped about *Chondrostoma toxostoma*: the number of rays in the dorsal and anal fins has in both cases decreased to 7.[1]

But a similar diminution in the number of rays in South European fishes may be likewise observed in other genera of Cyprinidae, very far distant from Chondrostoma in the system, namely, in bleaks (Alburnus), chubs (Leuciscus) and roaches (Rutilus). The European chub (*Leuciscus cephalus*) forms sub-species in Italy and the Caucasus, *cavedanus* in the former and *orientalis* in the latter. They both differ from the Northern chub in possessing a smaller number of rays in the dorsal and anal fins. The bleak, *Alburnus alburnus,* widely distributed in Europe, is replaced in Northern Italy by an allied species *A. alborella*, in Southern Italy by the nearly related species *albidus*, in the Northern Caucasus by the species *A. charusini*, analogous to the North Italian species, and in Transcaucasia by *A. hohenackeri,* corresponding to that of Southern Italy. The features by which these species are distinguished tend to develop in a determined direction, namely, in that of a diminution in the number of scales, of rays in the fins, in the length of the body, and in the number of vertebrae.[2]

But uniformity in the tendency is not confined to these features. The common line of variations affects coloration also: in certain South European and Transcaucasian species,

[1] See on this subject my "Faune de la Russie. Poissons," iii, part 2, 1914, pp. 361-366.

[2] See Berg, "Faune de la Russie. Poissons," iii, part 3 (in manuscript).

belonging to the genera Alburnus, Chondrostoma and Leuciscus, a dark pigment band may be observed on either side of the body. And yet another remarkable circumstance may be noted : in the western part of the Balkan peninsula the genera Chondrostoma and Leuciscus produce species with small scales, whereas in the species of the remaining parts of Europe the scales are large in these genera.

The representatives of the genus Alburnoides (of the Cyprinidae), within the area of their distribution, exhibit, following a west to east direction, the following series of definitely directed modifications: the anal fin of the typical European *Alburnoides bipunctatus* usually contains 14-18 branched rays, of the sub-species *fasciatus* from the Crimea, Northern Caucasus and Western Transcaucasia usually 13-15, and, finally, of the "natio" *eichwaldi* from Eastern Transcaucasia and Turkestan usually 11-13 rays.[1] Thus, in the direction from west to east the diminution of the number of rays of the anal fin in the representatives of the genus named manifests a compliance with a certain rule.

The European roach (*Rutilus rutilus*) is replaced in Italy and Dalmatia by the species *R. rubilio* (Bon.) (=*Leuciscus aula* Bon. et auct.), which is distinguished from the roach by its smaller size, by fewer vertebrae, by larger scales in the lateral line, and by a smaller number of rays in the dorsal and anal fins.

Leuciscus agassizi, distributed in the basins of the upper Rhone, Rhine and Danube, is represented in the north of Italy by the sub-species *savignyi*,[2] which differs from the typical form in the same way as *Rutilus rubilio* from *R. rutilus*.

The genera Leuciseus and Rutilus in the south of their geographical range in Europe and Western Asia, give origin to small-sized forms ; such, in the case of Leuciscus, are *L. borysthenicus*, *L. agdamicus*, *L. squaliusculus* and others (Berg, 1912, p. 92). Similar forms proceeding from the genus Rutilus have departed further from the initial type, and have therefore been separated into a distinct genus Phoxinellus (*l.c.* pp. 83-84).

[1] Berg, "Fresh-water Fishes of Russia," 1916, pp. 301-303.

[2] Fatio, i, p. 626.

Very many similar examples could be presented, but we shall confine ourselves to two more. The "vobla" (*Rutilus rutilus caspicus*), a Caspian sub-species of the roach, usually has 9 branched rays in the dorsal fin instead of 10, as in the roach and its sub-species *Rutilus rutilus fluviatilis*; that is, here again the number of rays in the southern forms is fewer; at the same time the number of scales in the lateral line is usually 43-44, *i.e.* it is less than in the European roach, which usually possesses 44-45. The Amur "id" (*Leuciscus waleckii*) is also distinguished by having a smaller number of rays in the dorsal fin (usually 7 branched rays) and of scales in the lateral line (usually 52-54), in comparison with the Siberian and European id (*L. idus*), which has 8 branched rays in the dorsal fin and 56-61 scales in the lateral line (Berg, 1912, pp. 171, 187).

All the foregoing shows that in a series of species far removed one from another in the system is observed a manifestation of a dominant rule whereby the number of rays in the fins is smaller in the southern forms than in the northern. This feature is, as a rule, combined in the southern forms with a smaller size, a smaller number of scales in the lateral line [1] and a more brilliant coloration. It is highly improbable, and indeed quite incredible, that in all the species named, belonging to separate genera, variations, which have led to the same results in all the species, should have arisen *by chance*.

On the theory of natural selection, the following explanation of this circumstance might be given. In the south it would be more useful for the fish to possess fewer rays in the fins, and consequently those varieties survive in the struggle for life which are accidentally endowed with a smaller number of rays than the northern forms. But such an explanation cannot be accepted for the following reasons:—

(1) Had varieties arisen by chance, deviation from the average in the south would be quite as frequent in the

[1] The small-scaled species, of which mention has been made, form a distinct, strictly localised group.

direction of a diminution in the number of rays as in that of an increase, and only the former deviations would be selected as being the more useful. But we actually find that in the south variations occur definitely in the direction of diminution. As an example, we may refer to the case of the roach, in which the number of the branched rays of the dorsal fin varies between 9 and 11, being usually 10, the limits for the "vobla" being 8 and 10, and the usual number of rays 9. Selection, if it does exert any influence, has thus other limits for its scope in the south from what it has in the north. Consequently, some kind of law must be present, owing to which a tendency towards a diminution of rays in the south is observed. This tendency is independent of the effects of selection, and the latter can only operate within the limits assigned by the former.

Therefore, we are faced with the question—*is the diminution in the number of rays due to selection, or is selection already confined in its scope by the pre-existing tendency towards such diminution?* The question of the effect of selection in producing this tendency could be raised only if the limits of variation were the same in the south and the north, *i.e.* 9 to 11. But as the limits are not the same, selection cannot be regarded as a primary agency in this matter.

This tendency, as we have seen, is subject to a certain dominant law, which it is easy to trace, if other species besides the roach and "vobla" be taken into account. It appears that several groups of species, living in approximately identical conditions, are subject to parallel variations. Consequently, a different course of evolution would be due to a different environment or geographical landscape.

(2) To the above the following objection might be raised from the point of view of selection. The predominance in the "vobla" of forms with a small number of rays is explained, not by such forms being born in larger numbers, (for no more are born in the south than in the north), but because the forms with a greater number of rays are not

adapted to live in the south, their mortality is greater, and in this way the predominance of the forms with fewer rays is obtained.

But such an objection is inadequate. Had forms with a greater number of rays in the south and with fewer rays in the north been more abundantly destroyed through selection, the curve of variation in adults, both for the north and south forms, would not resemble the curve of Quetelet, as it actually does. Let us illustrate this by an example. If the limits of variation for the fry of " vobla " were not 8-10 but 8-11, and if the variations 10-11 were chiefly to succumb, in the statistical enumeration of the adult voblas we would most often meet with 9, then not infrequently with 8, and very seldom with 10 or 11. As a matter of fact, the frequency of deviations in the direction of 8 is even less than in that of 10, while no specimens of vobla with 11 rays have been registered.[1] The voblas are thus born with the same distribution of deviations as are met with in the adults.

The principle noted above affects not only fresh-water, but also marine fishes. As has been indicated by Jordan (1905, pp. 202-217), in allied genera of marine fishes the northern forms possess a larger number of vertebrae than the southern. This holds good for a very large number of genera of the most diverse orders possessing nothing in common, as, for instance, for the flat-fishes (Pleuronectidae) and the anchovies (Engraulidae) : thus the northern flat-fishes have 50-60 vertebrae, while in the tropical ones the number of vertebrae falls to 35 ; the species of the tropical genus of anchovies Stolephorus have 40-42 vertebrae, whereas the anchovy Engraulis, inhabiting temperate regions, has 44-47. On the equator the coast fishes usually have 24 vertebrae, while the marine fishes below 60° latitude have as many as 60. A prevailing number of 24

[1] For the numerical data in the case of vobla see Pravdin, pp. 49, 65. (It must be observed that the author's actual figures are 8½, 9½, etc., which I have reduced to 8, 9, etc.).

vertebrae is found in a series of tropical (or mainly tropical) fishes, such as in the Sparidae, Chaetodontidae, Gerridae, Gobiidae, Pomacentridae and many other families, the number of vertebrae in the Plectognathi falling to 14; but in Lophius, also belonging to the Plectognathi, but inhabiting the temperate regions, the number of vertebrae rises to 30. It must be borne in mind that the number of scales in the lateral line bears a certain relation to the number of vertebrae.

We may conclude with another example from fishes. The sprats (*Spratella sprattus*) of the Baltic Sea are distinguished from the sprats of the North Sea by the same features as are the corresponding varieties of the herring (*Clupea harengus*): the head in the sprat of the eastern part of the Baltic Sea is lower and the snout longer than in the North Sea fish, these relations in the herrings of the Baltic and North Sea being the same (Heincke, pp. lxix-lxx).

2. THE EFFECTS OF THE LANDSCAPE ON THE BODILY CHARACTERS OF MAN

The distinguished American anthropologist, Boas (1911), has recently conducted some remarkable investigations on the variations that have affected the bodily (anthropological) characters of the descendants of European settlers in America. The extraordinary results which have attended the researches of Boas have not hitherto attracted the attention of zoologists and botanists, and yet they help to throw much light on the question with which we are dealing.

Boas has examined Jews and Sicilians born in America—of Jews, 4105 men and 1888 women; and of Sicilians, 1767 men and 1746 women. The Jews from Eastern Europe, the descendants of whom have been examined in America, have a rounded, brachycephalic skull and a mean cephalic index of 83. Their descendants (the children of immigrants), born in America, have become more dolichocephalic, their mean cephalic index being 81. Such a result is in itself remarkable; but it becomes more so if it

be compared with what has been shown in the case of Sicilians. The Sicilians in their own country are dolichocephalic, having a cephalic index of 78; in America their descendants become brachycephalic, acquiring an index of 80.

Thus, in the descendants of Jews and Sicilians in America, development follows contrary directions, ultimately resulting in a type of skull with a nearly identical index of 80-81. Both Jews and Sicilians, under the effects of the American geographical landscape, approach a certain uniform type. Such a phenomenon very much recalls mimicry.

The influence of American conditions upon the descendants of immigrants grows in proportion to the length of time that had elapsed between the emigration of the parents to America and the birth of the child: the longer the parents have lived in America before the birth of the child, the more the child differs from the European type. Thus, the cephalic index in Sicilian boys of 5 to 12 years old, immigrants to America, has proved to be 79·5, in Sicilians (5-19 years old), born in America less than ten years after the immigration of the mother into that country, 80·9, and in those born ten years or more since the mother's immigration, 81·8.

The variations displayed by the descendants of immigrants affect not only the cephalic index, but likewise height [1] and weight of body, length and breadth of head and breadth of face. In Jews born in America height, weight, and length of head increase; the breadth of the head and face diminishes. In Sicilians born in America, on the contrary, height, length of head and breadth of face diminish, while the breadth of the head increases.

The third type, also examined by Boas, includes Bohemians (Tchekhs), Slovaks, Poles and Hungarians. They also exhibit variations, and, what is remarkable, *all* in one direction: the cephalic index diminishes in all.

It is noteworthy that the generation of immigrants born

[1] As regards increase in the height of emigrants to America, we find certain indications in Darwin's "Descent of Man," chap. vii.

in Europe display no modification, however long they may have resided in America. Jewish children brought to America even at the age of one year old exhibit no differences in the cephalic index as compared with Eastern European children, it being about 83. But the index at once drops to 82 in children born immediately after the arrival of the mother in America and to 79 in the case of the second generation, *i.e.* in the grandchildren of settlers. "In other words," says Boas (p. 61), "the influence of the American environment is manifested in the descendants at once; it slowly grows in proportion to the time that has elapsed since the immigration of the parents to the birth of the child." The same is the case *mutatis mutandis* with Sicilians (see Boas, table on p. 61).

It must be borne in mind that the modification of characters affects *all the individuals*.

A similar example is afforded by the Basques. The French Basques, like the surrounding French population, are brachycephalic, with a mean cephalic index of 83; within the confines of Spain, on the contrary, this people are dolichocephalic (index 79) like the neighbouring Spaniards.[1] It is to be supposed that the original type of the Basques was brachycephalic, as in France they are broader-headed than the French of Bearn, and in Spain they are less dolichocephalic than their neighbours the Spaniards.

These observations exhibit an unusual plasticity of the human organism. After the researches of Boas it is no longer possible to attribute to brachy- and dolicho-cephaly that importance in the classification of the different races of mankind that they were formerly supposed to possess. Ripley, for example, regarded (1900, p. 52) the shape of the skull as a very convenient systematic feature, the head form being immune from all disturbance from physical

[1] Ripley, p. 191 and map on p. 189. This author presumes (p. 197) that the Spanish Basques are a cross with Spaniards. Such a suggestion, in view of the notorious estrangement of the Basques, is very improbable.

environment. Neither climate, food, economical status nor habits of life, in Ripley's opinion, are able to produce any effect on the shape of the skull.[1] How out-of-date such arguments seem in the light of recent facts!

In American immigrants, it may be presumed, the shape of the skull is modified in the direction of an approximation to that of the natives. But such is also the case with regard to other characters.

In that respect Jews, who are distributed all over the world amid kindred races, offer a grateful field for investigation. Now, it appears that the physical type of Jews universally more or less approaches the type of population by which they are surrounded. By this we do not mean to say that the physical type of the Jew, as a definite taxonomic unity, is modified: Jews anthropologically remain Jews, but certain of their characters vary in a *determined direction*, namely, in approximating to the type of the indigenous population.

With such a reservation we may proceed to consider certain facts having a relation to the matter.

The Caucasian Jews, like the people among whom they live, are extremely brachycephalic; the cephalic index of Daghestan Jews is 86·3. North African and Arabian Jews, like the surrounding peoples, are, on the contrary, dolichocephalic, possessing a mean cephalic index of 78·2 (Fishberg, pp. 49, 50).

In Daghestan nearly half are hyper-brachycephalic, in Europe meso- and sub-brachycephalic, in North Africa hyper-dolicho- and dolichocephalic, and in Yemen 72 per cent. are hyper-dolichocephalic.

As regards Europe, a comparison of the skulls of Jews and the non-Jewish population exhibits a parallelism in the cephalic index.

Fishberg is inclined to think (p. 56) that the similarity in the cephalic index of Jews and of the people by whom they

[1] Cf. also p. 50.

are surrounded is due to the intermarriage of Jews with natives. But such a supposition is quite incredible, and is refuted by many authors who have written on the subject.

With reference to the facts presented by Boas, E. Auerbach (1912, pp. 607-608) evolves the following arguments. Johannsen assumes that the greater the absolute length of the skull the more prone it is to become dolichocephalic.[1] Therefore, in individuals with a large head, *i.e.* who are tall, dolichocephaly would be more clearly manifested than in individuals of short stature.[2] It is East European Jews of a high stature that emigrate to America ; [3] there is, therefore, nothing wonderful in the fact that their descendants should possess longer skulls than the Jews of Eastern Europe. All this is perfectly just. But in this matter Auerbach lost sight of the circumstance that Boas had measured, not only Jews born in America, but also American Jews born in Europe, and these latter prove to be more brachycephalic than the first generation born in America. It is thus immaterial whether taller or shorter Jews emigrate to America ; what is important is that the first generation born in America becomes more dolichocephalic. And this fact was pointed out in the first pages of Boas's book.

The results obtained by Boas are open to the interpretation that round-headed Jews and long-headed Sicilians, born in America, are subject to a relatively higher mortality. By this means, *i.e.*, through the effect on natural selection, the relative long-headedness of American Jews and short-headedness of American Sicilians could be accounted for. The possibility of such an explanation is indicated by Boas (p. 75). To this cause (selective mortality) variations in the shape of the skull are referred by Fehlinger, in proof of which he adduces (pp. 20-21) the circumstance

[1] Such is also the opinion of Pearson.

[2] To this an objection is raised in the case of Italians (see C. Bresciani-Ferroni) and Bavarians (see Fehlinger, " Pet. Mitt.," 1913, ii, p. 22).

[3] The same is true of the Scots : Scotch immigrants to America are on the average two inches taller than their kindred in Scotland (Ripley, p. 89).

that the number of long-headed Jews increases with age. But the fact remains that a diminution in the cephalic index with advancing age is observed in European Jews as well as *in their American descendants. And there are no facts to* prove that the greater long-headedness of American Jews is due to a greater mortality in America of short-headed Jews. *Besides, it has not been observed in Sicilians that they* become more short-headed with advancing age.

The colouring of the hair and of the eyes of East-European Jews, although darker than that of the neighbouring peoples (not Jews), is still much lighter than that of the Jews of Syria and Palestine (examined by Weissenberg): in the latter black and brown eyes occur in 80 per cent., whereas among European Jews, according to Elkind, only in 49 per cent. Both in regard to pigmentation and the cephalic index, "European Jews occupy a kind of intermediate position between the Jews of Palestine and the Christian population of Europe": the cephalic index of the European Jews is 1-2 units below that of the non-Jewish population, and 3-4 above that of the Jews of Palestine. A similar approximation of Jews to Europeans may be observed in the facial (in Europe somewhat broader-faced) and nasal index (in Europe somewhat broader-nosed). The "semitic" shape of the nose is more frequently met with in the Jews of Asia Minor than in those of Europe. As has been ascertained by Elkind (1908),[1] "the present state of our knowledge regarding the physical peculiarities of European Jews enables us from an anthropological point of view to maintain that in them we meet with a type occupying a kind of intermediate position between the Jews of the Mediterranean region and the Christian population of Europe, a type which is fairly uniform, and in spite of local deviations is characterised by certain definite distinctive features."

[1] "Versuch einer anthropologischen Parallele zwischen Juden und Nicht-Juden." Zeitschr. f. Demogr. und Statistik der Juden, iv, 1908 (not seen by me; quoted after Bunak, 1922).

Besides the observations of Boas, we have quite recently obtained remarkable figures from Bolk (1914) concerning an increase in height in the Dutch and in Dutch Jews for the last decades. The author examined 422,629 recruits in Holland for the period 1898-1907, and it appears that in all the provinces of the kingdom a marked increase in height had been manifested (p. 37).

Yet more remarkable results are obtained when the figures for the middle years of last century are taken for comparison. In the town of Zaandam near Amsterdam, of 138 nineteen-year-old youths 69 (*i.e.* 50%) were below 157 cm. in height in 1858, while in 1907, of 240 youths of the same age only 6 were below 157 cm., and 141, or 58·7%, were above 170 cm. height. In other words, the average *height has increased by more than 13 cm. during the half* century. Such changes are generally attributed to an improvement in the general conditions of life; the prosperity of the Dutch, however, is, according to Bolk, much *the same as it was fifty years ago. Thus the cause of the* phenomenon referred to is obscure.

But what is a matter of particular interest to us is the simultaneous increase in height in such different races as the Dutch and Dutch Jews. In Amsterdam the average height of recruits was (p. 46) :—

	In centimetres.		
	1850.	1900.	Difference.
Christians -	158·5	169·4	+10·9
Jews - -	156·5	162·9	+ 6·4

It is noteworthy that the same phenomenon, *i.e.*, increase in height, is observed in Denmark, Sweden and Norway. Thus the average height of recruits in Denmark in the years 1852-56 was 165·4 cm., in 1909-10, 169·5; in Sweden in 1841-45, 167·3 cm., in 1887-94, 169·5 cm.; in Norway in

1854-59, 168·6 cm., in 1904-05, 170·5 cm.[1] The same has been shown for Germany in recent years, and still earlier by Ammon with special reference to Baden.

The shores of the Baltic Sea have for long been inhabited by several peoples, very far removed from one another in point of language and other features. They are Slavs, Letts, Esthonians, Finns, Swedes, Danes and Germans. All these peoples, to whichever of the above races they belong, possess fair hair and blue eyes.[2]

It is a case of a peculiar kind of "mimicry."

Byron says, "As the soil is, is the heart of man." But it appears that not only the human soul depends upon "soil," but the entire physical structure of man bears a marked impress of the general physico-geographical environment.

A certain analogy with the facts supplied by Boas is presented by the experiments of Goebel on plants. If a seed of *Ranunculus purshii* (=*R. multifidus*) with tripartite leaves be sown in water, a plant with filiform leaves will be obtained, very much resembling the leaves of the aquatic *Ranunculus divaricatus*; such a modification is, of course, not hereditary, *i.e.* with a change of the medium the plant reverts to its former condition.

Let us take another example from the world of plants. On the Amur and in Manchuria two lime-trees are distributed, (1) *Tilia amurensis* Kom., closely allied to the European and West-Siberian *T. cordata* Mill., and (2) *Tilia mandshurica* Rupr. et Max., replacing the West-European *T. argentea* in the Far East. "It is remarkable," says Komarov (1907, p. 30), "that both lime-trees occurring in Manchuria are distinguished from their allied European forms by one and the same constant feature, *i.e.* less frequent and deeper indentations, furnished with long hard points."

[1] K. Wieth Knudsen, Arch. f. Rassen- und Gesell.-Biologie, ix, 1912, p. 192.

[2] This circumstance has been pointed out to me by Semenov-Tian-Shansky.

This is perfectly analogous to the diminution in the number of the rays in the fins of the Cyprinidae of Southern Europe, as compared to those of the North of that continent.

We do not mean, of course, that forms removed to a new landscape will always vary in a corresponding manner. We know of a number of plants transported from America into Europe, which have nevertheless obstinately preserved their original characters. To such belong, for example, *Erigeron canadense* and many others (de Vries, 1906, p. 426). Forms may be mentioned which have persistently preserved their individuality, at least throughout the short period of time during which we have studied them. Some Siberian conifers, sub-species of corresponding European trees, upon being transplanted into Europe, continue to preserve their phenological peculiarities. The plaice (*Pleuronectes platessa*) of the North Sea grows more rapidly than the Baltic form; on being removed from Heligoland to Kiel, it nevertheless preserves its rapid growth, a feature which is highly characteristic of the North Sea sub-species. According to the researches of Gaidukov, blue-green algae, on being submitted to the rays of the spectrum, assume complementary colours: they become red in the green rays and green in the red; on being removed to normal conditions in the process of reproduction, they at first produce cells coloured in the complementary colour.

Sumner (1915) removed the Californian field-mouse *Peromyscus maniculatus*, sub-species *sonoriensis*, from Victorville to Berkeley. Both places are in California, but the first is in the desert, where the annual precipitation is 150 mm. and the mean relative humidity is 45%; while Berkeley lies on the sea coast, has an annual precipitation of 650 mm. and a mean relative humidity of 83%. Berkeley is the home of another sub-species of the Californian mouse, sub-species *gambeli*. Now, it appears that neither the specimens of *sonoriensis* removed to Berkeley, nor their children and grandchildren, exhibited any perceptible approximation to the

type of the local sub-species *gambeli* ; throughout the whole time they were under observation they continued to belong to the sub-species *sonoriensis* (these two sub-species differ in coloration).

Thus it may be possible that for certain forms the effects of the landscape must accumulate for some time, in order to be manifested in a burst of enhanced variability. Others react rapidly. On the other hand, if the landscape remains invariable, many forms have no occasion to be modified. In the pyramids of ancient Egypt many plants have been found which grow at present on the shores of the lower Nile, and they in no way differ from the recent forms

3. DOMESTIC ANIMALS

I have searched among domestic animals for cases analogous to what has been described by Boas for man, but I have succeeded in coming across only a few indications. Neumayr (1889, p. 128, note), following Wilckens, relates that Swiss cattle, on being removed to Hungary, acquire certain features of the local Hungarian cattle, namely, long horns and legs. Wilckens himself, in his work on the Central European breeds of cattle (1885, pp. 11-12), which had appeared somewhat earlier, mentions the following case.

Cattle were brought from Algäu, Bavarian Alps, into the crown estate of Altenburg in Hungary. Wilckens examined two generations of this cattle born in Hungary from pure-blood Algäu parents. It appeared that their horns had increased in length, become harder and acquired a peculiar lyre-like form, all of which are features characterising the local Hungarian breed (which, as is known, is closely allied to the Russian grey steppe cattle) ; at the same time, the skull became relatively narrower, and the milk productiveness less.

Hence Wilckens concludes that " the peculiar shape of the body of the Algäu cattle, through the effects of the

climate and soil of Hungary, has varied in the direction of Hungarian cattle." The same thing is confirmed by Kronacher (iii, 1917, pp. 127-128).

The number of individuals which were examined by Wilckens is, of course, insignificant. But the data obtained are reliable.

Shorthorns, bred in Uruguay (Artigas), assume the outward appearance of the native race of cattle, the so-called "criollos." Simmental cows, purely bred in Hesse (Vogelsberg), in three generations became indistinguishable from the native Vogelsberg cattle (Kronacher, *l.c.*, pp. 128, 129).

Animal breeders know that horses in dry steppes and in deserts are slender, nervous, swift-footed and relatively small. A moist climate and succulent food, on the contrary, contribute to the formation of draught animals. On being removed to a dry climate, draught horses dry up, as it were, and lose their peculiar characters. Fine-fleeced sheep come from dry and warm climates ; if they be transported into a humid climate, their wool becomes coarser and longer.

4. FURTHER EXAMPLES

1. In complete accordance with the results obtained by Boas may be noted the observations of J. Schmidt (1920) on the viviparous fish *Zoarces viviparus*. In this case also the effects of the environment were displayed in the progeny. The investigation was carried out in Danish waters, in Ise Fjord and Roskilde Fjord on the north coast of Sealand. The average number of vertebrae in populations of *Zoarces viviparus* from different parts of the fjords was not the same : it was 108·0 for that from Station No. 34, and 114·6 from Station No. 69. In 1916 and 1917 the following transplantation experiments were carried out. A large number of the fish were conveyed in early summer, while the sexual organs were still unripe, to the neighbourhood of Station 31 in four large wooden boxes. When the

experiment was brought to a conclusion, the total number of gravid females was 119. Examination showed that the average number of vertebrae in 1190 embryos taken from the transplanted 119 mothers was 114·5, whereas the corresponding feature in the case of the non-transplanted samples of the same population was 113·1 in 1916 and 113·2 in 1917. "It is therefore evident that the external conditions, altered through the transplantation, have decidedly raised the average number of vertebrae in the population" (p. 184).

It may further be noted that the number of vertebrae is a character determined by internal causes, being, in other words, hereditary. From Schmidt's tables it is evident that mothers with a large number of vertebrae (say 116) produce an offspring with an increased number (namely 114·14), whereas in the offspring of mothers with fewer vertebrae (say 110) a reduction in the number of vertebrae occurs (namely 111·58).[1]

Another analogous case has long been known. In 1870 J. Boll transported from Texas to Switzerland (Canton of Aargau) cocoons of the lunar moth, *Saturnia luna* (or *Actias luna*), a beautiful silk-worm moth belonging to the Saturnidae. In America the caterpillar of this species feeds on the leaves of the hickory (Carya) and the black walnut tree (*Juglans nigra*). In May, 1871, from the cocoons that had hibernated in Switzerland, emerged moths that were indistinguishable from the American typical form. Some of these moths laid eggs, and the caterpillars of this European generation fed on leaves of the European walnut (*Juglans regia*). They became pupae in the end of June, which early in August produced 35 moths. These latter most unexpectedly

[1] There is nothing surprising in the circumstance that the offspring of mothers taken in normal conditions should exhibit a number of vertebrae differing from that of their mothers, as the father in every single case remains unknown. As the material is large, says Schmidt, we are enabled to assume that the paternal number of vertebrae is in the mean equal to the average of the population, namely 113·2.

exhibited so many points of difference from their maternal American form that they were described as a new species, *Saturnia bolli.* They differed in form, as well as in pattern and coloration : the body and wings were larger and heavier, the antennae narrower, the longitudinal carmine stripe on the abdomen had disappeared, and the moth became lemon-yellow, instead of yellowish-green. The carmine marginal stripe on the anterior wings had quite disappeared. (M. Wagner, 1889, pp. 307-310.)

2. During the Pliocene in the south-east of Europe there were many large brackish-water lakes, which gradually freshened in the course of time, this latter circumstance finding confirmation in the disappearance of salt-water Mollusca from the most recent deposits of these lakes. Now, in these a remarkable transformation in the shells of Mollusca frequently belonging to different families, and even to different classes, may be observed. On the shells of Vivipara, Melanopsis, Bythinia, Neritina, and Unio appear peculiar nodules, ribs and thickenings, such as may be observed to occur in Slavonia, Roumania, the island of Kos and elsewhere. Neumayr (1889, p. 128; 1875, p. 102) attributes this modification to the freshening of the water in the lakes. He adds (1875, p. 102) that there is no ground for regarding this phenomenon as being due to natural selection.

But a similar effect is produced when the body of water becomes salt. Thus, according to Dall, in many genera of Mollusca from the Pliocene and Quaternary lacustrine marls, which have been deposited in the drying lakes in Utah, Nevada and California, may be observed a gradual complication in the sculpture of the shells. This phenomenon is manifested, according to Dall's expression, "unanimously," whatever the systematic group to which belong the Mollusca under examination. This complication in the sculpture of the shells becomes ever greater in the successive layers of marls, as we gradually ascend from the older to the more recent deposits.

But the same may be observed to occur in the shells of recent fresh-water Mollusca, which breed in artificial salt basins such as those in Nevada.[1] The brackish water of Lake Utah is inhabited by a pond snail, *Galba* (*Polyrhytis*) *utahensis*, in which the shell is not smooth, as in all the other living Lymnaeidae, but has conspicuous longitudinal folds and ribs (in certain specimens, however, the sculpture is all but absent). This species much resembles the pond snail described from the Lower Pliocene deposits of Utah under the name *Lymnaea kingi*, and referred by Baker to the same sub-genus of Polyrhytis. It is remarkable that Polyrhytis, in so far as the sculpture of the shell is concerned, occupies the same position with regard to Lymnaea, as Costella does to Physa ;[2] the latter is not included by Baker in the family of Lymnaeidae (although Physa is commonly referred to the sub-family Physini of the family Lymnaeidae).

In Darwin's " Variation of Animals and Plants," among many examples of " direct and definite action of the external conditions of life " (chap. xxiii), the following may be found : young oysters brought from Wales and placed in beds inhabited by local (" native ") oysters, in about two months begin to acquire the appearance of the latter. Young oysters taken from the shores of England and placed in the Mediterranean at once altered their manner of growth, and formed prominent diverging rays, like those of the shells of the proper Mediterranean oyster (ii, p. 280).

All Caspian Cumacea belong to the family Pseudocumidae, to which only one marine genus is to be referred. Some Caspian Cumacea exhibit a perplexing similarity to marine Cumacea belonging to different families. Thus the Caspian *Stenocuma diastyloides* Sars recalls certain species of the marine genus Diastylis, *Schizorhynchus eudorelloides* Sars is very similar to the marine Eudorella, and Caspiocuma

[1] Dall, 1896, quoted after Baker, p. 30.

[2] Baker, pp. 458-460, 29, 86, 102.

Sars "mimics" the marine genus Campylaspis Sars, which belongs to a very different family of Cumacea (Sars, 1914).[1]

Dorogostaisky (1922, p. 107) investigated the Gammaridae inhabiting Lake Baikal near the Selenga delta. It appears "that the peculiarities in the structure of the Selenga forms by which the latter differ from the typical ones, in the case of even the most widely (systematically) separated groups of the Gammaridae, are nearly of the same order." Namely, (1) in all the species living near the Selenga delta the coloration is not so bright, the yellow and green tints being replaced by brownish ones; thus, *Pallasea grubei* is greenish, while *P. grubei arenicola* is brownish; *Carinurus solskii* yellowish, *C. solskii obscurus* brick-red; the black spots of the typical forms are replaced by brownish or greyish spots. (2) The dermal processes on the body are much reduced in the Selenga forms. (3) The surface of the body, of the lateral laminae and extremities is in these forms rougher, the spines and hairs are more strongly developed on the body. (4) The antennae are not so long and are more massive. In other parts of Lake Baikal these forms have not been found: they seem to be endemic to the Selenga delta region. The writer lays stress on the peculiarity of the local conditions which affect all forms, characterised by a muddy and sandy bottom and a higher temperature, an insignificant depth, lesser transparency, and, evidently, a peculiar chemical composition of the water.

Zernov, an authority on the fauna of the Black Sea, says (1913, p. 242) that he, as well as Milashevich (a well-known conchologist), is able to pick out Black Sea specimens from a heap of Mediterranean and Black Sea representatives of one and the same, or nearly allied, species—oysters, for instance. The same test is applicable to other representatives of the Black Sea fauna, as, for example, to the higher Crustacea. "On nearly all Black Sea animals lies a certain

[1] My attention was drawn to the above-named paper of Sars by A. N. Derjavin.

'Black Sea imprint': reduced size (with the exception of several species of a more northerly origin), a paler hue, a poorer sculpture, a decreased transparency, etc."

The deep-water Mollusca (Gastropoda) inhabiting the deep fresh-water lakes Baikal and Tanganyika (the depth of each is about 1500 metres) have in both lakes acquired a peculiar sculpture, approximating them to marine genera and to the above-mentioned Pliocene forms of South-eastern Europe.[1]

The common grass-snake *Tropidonotus natrix* is represented in the south (in South-eastern Europe, in the Caucasus, in Western Asia) by a sub-species (*persa*), which is distinguished by the presence on its back of two longitudinal narrow stripes of a yellow or white colour. The viperine grass-snake, *Tr. viperinus*, forms a similar variety (*aurolineatus*) in Algeria.

3. In an important paper, devoted to the question of morphological parallelism, Semenov (1900) has called attention to the following circumstance. The beetle Ametor, belonging to the family Hydrophilidae and found in the Samarkand province, Turkestan, is in outward appearance unlike its kin, and more nearly approaches representatives of the families Tenebrionidae or Trogositidae. Though exhibiting a very peculiar appearance, this beetle is, nevertheless, closely allied to the genus Hydrobius of the family Hydrophilidae. But what follows is very remarkable. In the mountains of the same Samarkand province occurs a water-beetle, Hydronebrius, belonging to another family, the Dytiscidae. This Hydronebrius, allied to the genus Agabus, has the same outward appearance as Ametor, quite distinct from its nearest kindred the Dytiscidae: it has the same coarse sculptured integument, with the surface all but completely dull, and a depressed prothorax. Both Ametor and Hydronebrius have a posteriorly narrowed prothorax

[1] On the Mollusca of Baikal see Lindholm, 1909; on those of Tanganyika, Cunnington, 1920, pp. 542 *seq.*, 550.

(whereas all the other water-beetles have the prothorax posteriorly dilated). Two aquatic beetles belonging to different families have thus acquired in the province of Samarkand a very similar outward appearance, quite distinct from the other representatives of their respective families. Semenov describes this phenomenon as "morphological or morphomatic parallelism," meaning by this term the "tendency in separate species independently of their genetic affinity to develop in the same determined direction through the influence of analogous or identical conditions, thereby acquiring a complex of common characters (progressive or regressive)" (p. 621).

4. *In animals inhabiting sandy deserts a resemblance in the structure of the limbs may be observed.*

This matter formed the subject of the investigations of Faussek (1906) in the Transcaspian province. In many sand-lizards the toes are fringed with horny indentations. This peculiarity occurs in *Phrynocephalus mystaceus*, *Ph. interscapularis* (Agamidae), *Scapteira grammica* (Lacertidae), as also in the geckos *Teratoscincus scincus*, *Crossobamon eversmanni*.[1] Such a contrivance is believed to be an adaptation to progression in moving sand: the fringe is supposed to prevent the animal from sinking in the sand, by acting as a kind of sand snow-shoe. Faussek believes that it also assists the animal to scatter away the sand (p. 14). The contrivance described is possessed only by lizards inhabiting moving sands; it is specially elaborated by species living in sand, and, as we have seen, independently of the taxonomic family to which a given genus belongs. Within the limits of a genus, as, for instance, of Phrynocephalus, species not inhabiting sand are destitute of the contrivance referred to.

But exactly similar adaptations are displayed in the extremities of other sand-inhabiting animals.

[1] The same peculiarity is observed to occur also in the South African gecko Ptenopus and in the North American iguana Uma (cf. Cope, 1896, p. 73).

Thus, among the Tenebrionidae, beetles with very characteristic representatives in deserts, occur forms exclusively peculiar to sandy regions. In *Sympiezocnemis gigantea*, not infrequently met with in the sands near Askhabad, Transcaspia, the tarsus and the distal end of the tibia of the second and especially of the third pairs of legs is densely covered with long chitinous hairs. By the aid of these contrivances the beetle is enabled, as with a brush, to scatter the sand. But in addition, the fringe of hairs affords the insects a supplementary hold for walking on shifting sand.[1]

An exactly similar structure is observed in many other sand-beetles: in Trigonoscelis, *Sternodes caspius*, *Argyrophana deserti*, etc. The hairs on the legs of the sand-beetle *Scarites bucida* of the family Carabidae are very much developed. We meet with the same contrivances in wasps burrowing in sand, as, for instance, in *Pompilius kizilkumensis*, which may be found in the vicinity of Askhabad (Faussek, pp. 31-33). "The same contrivance for scattering sand, rows of hairs constituting a kind of hrush, may be produced quite independently and spontaneously in different genera, families and orders of insects; it may be formed either on the first, the second or the third pair of legs, on the tarsus or the tibia, according to the method in which the insect employs its legs in burrowing in the sand" (p. 34).

In mammals, the toes of *Ellobius talpinus* are covered like a brush with numerous hairs; the same occurs on the fore-limbs of the sand souslik, *Spermophilus leptodactylus*.

Besides the above-mentioned "foot brush," in many sand-loving animals we observe contrivances for affording a better hold for progression in sand.

To such may be referred the "padded foot" of the camel and the bird *Syrrhaptes paradoxa*, the tibia of the beetles Rhizotrogus (Chionosoma), Cyphonotus, Eutyctus (all three of the family Scarabaeidae), the spined tibia of the sand cockroach *Polyphaga* (*Heterogamia*) *aegyptiaca* (Faussek, p. 53).

[1] Faussek, pp. 19-20.

5. Various species of bumble-bees in the Caucasus acquire white dorsal bands. Such bands are met with in *Bombus* (*Cullumanobombus*) *apollineus*, *B.* (*Lapidariobombus*) *incertus* and *B.* (*Alpigenobombus*) *alpigenus*. And yet bumble-bees inhabiting low ground and corresponding to the two first-named species do not have these white bands on the back ; such are *B.* (*Cullumanobombus*) *silantjevi* and *B.* (*Lapidariobombus*) *lapidarius* (Skorikov).

In South America, in certain localities, Hymenoptera of various groups have a brownish pubescence, and in Australia the usually light yellow colour of many Hymenoptera is turned into ochreous yellow. It has been observed that in many places butterflies of different groups have a similar coloration, while in others the same genera very considerably differ from one another ; thus, the butterflies of Java are distinguished by their dark colour. According to the observations of Bates, many species of butterflies in the Amazon Valley vary in coloration in an analogous manner according to locality. This is also confirmed by Seitz (1891, pp. 317-318). In the forests of Southern Brazil he came across a locality where the butterflies were distinguished by having a brilliant blue coloration. Out of twenty species one-half was totally blue, the remainder partially so.[1] Such a uniformity in colouring not only affected butterflies, but extended to beetles, Hemiptera and even Diptera. It is remarkable that the preference accorded by nature to blue coloration was confined to a small district ; several miles to the north of that place the blue kingdom ceased, and was replaced by a red one. Seitz further points out (p. 317) that, according to the observations of Ransonnet and Haeckel, green prevails among the animals of Ceylon. Of a couple of dozen insects caught at random while flying round some bush, hardly a single one would be found that did not exhibit green in some degree, as being its funda-

[1] Morpho, *Myscelia orsis*, *Anaea stenyo*, *Heliconius apseudes*, Eurybia, Pythonides, etc.

mental colour ; at the same time may be seen green butterflies of the groups Sarpedon and Paris, *Papilio agamemnon* and Danaidae. It is worthy of notice that many marine animals off the coast of Ceylon are remarkable for their green colour.

> The European *Colias edusa* produces a variety *helice* ; a corresponding variety departs from its maternal Argentine form *Colias lesbia* in the very same direction of structure. Wallace discovered wings of a peculiar shape in a number of Papilionidae and Pieridae from Celebes : the anterior margin is extended bow fashion, with the apices of the wing produced forward. The butterflies of India and the Malay Archipelago are generally distinguished by the peculiar form of the wings. The Australian butterflies, on the contrary, are characterised by their pubescent thorax and head. In South America the Heliconidae and Neotropidae are conspicuous for their slender shapes, dragon-fly wings and coloration in parallel stripes. The same coloration is peculiar to many South American butterflies.[1]
>
> Punnett in his book "Mimicry in Butterflies" (1915, pp. 134-135) points out that some types of coloration recur in different genera and families of butterflies in certain geographical regions of South America. In Central America a certain pattern (horizontal and oblique black bands on a bright fulvous brown ground, with two broken yellow bars towards the tip of the fore-wing) is displayed, which is common to many Heliconini, Ithomiini, Nymphalini and Pieridae. In Eastern Brazil the same butterflies exhibit another pattern, but that one is likewise common to them all. On the Upper Amazon a third type of coloration is met with, which is peculiar to nearly all the same genera. Lastly, a fourth pattern is found in Ecuador, Peru and Bolivia in nearly the same combination of genera.

In the New World, especially in Central America, snakes with red-black-yellow rings (the so-called elapoid coloration) are very common, this coloration being very rare in the Indo-Malayan region, and practically absent in Africa.

[1] Seitz, pp. 319, 322.

Referring to this fact (as also to the presence in Tropical America of mammals with a prehensile tail belonging to totally different orders) Gadow (1911), in answer to the question why that should be so, says, " because the American environment favours the production of red in snakes " (p. 22).

Neumayr (1899, p. 127) observes that along the west coast of South America nearly all the marine Mollusca exhibit a blackish colour, and nearly all the Eocene marine Gastropoda from one of the deposits of Australia, although belonging to different genera, are characterised by a very *prominent nucleus*.

Beetles inhabiting the sands of Central Asian deserts, and representing different families, are usually of a pale ochre, whitish or reddish colour, and many possess a more or less transparent integument. Certain Buprestidae and Tenebrionidae inhabiting sandy deserts have the brilliant metallic coloration distinguishing these families concealed beneath a layer of scales, hairs or a peculiar pulverescent exudation (Semenov-Tian-Shansky, 1913, pp. 269-270).

In a similar manner many African animals are distinguished by their yellow or yellow-brown colour ; such are the butterflies Hypanis, Crenis, Acraea, *Danais chrysippus* and many others (Seitz, p. 321). *A tendency is thus generally* manifested to produce similar forms in similar landscapes.

6. The plankton organisms display certain common contrivances enabling them to keep on the surface of the water, and to resemble in colour the medium which they inhabit : they possess processes (Radiolaria, Rotatoria, Crustacea), are supplied with gas vacuoles for floating (Arcella, *Difflugia hydrostatica*, many Cyanophyceae), their skeletal elements are delicate (Foraminifera, Algae, Mollusca), the body becomes transparent (Medusae, Mollusca, Crustacea, the larvae of fishes, especially of eels—"Leptocephalus,"—the eggs of many fishes, especially of the anchovy (Engraulis), Rotatoria, Tunicata, Sagitta, larvae of insects, such as Corethra, etc.).

5. PLANTS

Plants exhibit numerous instances of similar development under the influence of similar external conditions. In the Alpine zone of mountains and in the Arctic and Antarctic regions many plants, such as *Draba alpina*, Azorella and others, acquire a cushion-like growth. Out of 23 species from the extreme north-east of Siberia, 13 form cushions. To polar plants, belonging to the most diverse families, a dwarf growth and firm, leathery leaves are peculiar.

Plants growing on a calcareous soil are distinguished by the following features from their kindred inhabiting other soils (Warming, 1918, p. 81): they are more hairy, are not infrequently covered with a white or grey matted coat, bear blue-grey, deeply dissected leaves, and have flowers with a larger and paler-coloured corolla.

Among aquatic plants many are entirely destitute of roots (Salvinia, Wolffia, Ceratophyllum, *Utricularia vulgaris*, Aldrovandia, etc.); in others, roots are rudimentary, or else the rootlets are deficient; the vessels and the xylem are rudimentary, the mechanical tissue is either reduced or is not developed; the pneumatic system, on the contrary, is usually well developed; the epidermis is thin, hairs and stomata are usually lacking; leaves in submerged flowering plants are divided into filiform lobes (Utricularia, Ceratophyllum, Hottonia and others) (Warming, pp. 203-207); in floating plants the runners have short internodes and are generally shortened, while the leaf blades are very broad, being peltate, cordate or ovate (Hydrocharis, etc.) (Warming, p. 356). Representatives of the most various families of aquatic flowering plants produce winter buds: *Potamogeton crispus*, *Hydrocharis morsus-ranae*, *Hydrilla verticillata*, *Sagittaria sagittifolia*, *Utricularia vulgaris* and others (Griesenhagen, p. 318; Neger, pp. 274-275).

Xerophilous plants are very peculiar. To avoid needless evaporation, many of them are completely destitute of

leaves, and, as a consequence, such remarkable examples of convergence as the American Cereus and Opuntia, and the African Euphorbiaceae (such as *Euphorbia canariensis* with the aspect of a Cereus) are produced.

Halophytes plants are conspicuous for their thick and fleshy leaves; they are generally devoid of hairs (in sands pubescent species occur). They do not grow high, their stems often being procumbent. Their leaves are commonly undivided, with an entire margin. They usually possess no spines.

Mangrove vegetation, belonging to most diverse families, exhibits similar characters.

Many more cases of a similar kind could be mentioned in confirmation of our assumption, that the geographical landscape exerts a like effect on the organisms subject to it.

And yet the following objection to this assertion might be urged. The organisms that we have mentioned above, such as halophytes, for instance, possess a complex of features peculiar to them, not because they have actively adapted themselves to live on a saline soil; on the contrary, they have established themselves on that soil because they were previously endowed with suitable features. Such a point of view is not absolutely antagonistic to our opinions: in many cases we ourselves are ready to support it (see chap. iii, section 5). We know, however, numerous cases of a direct adaptation of plants to the environment. In cultivating plants in a soil rich in salts, Lesage revealed modifications in the organs assuming the appearance of halophytes: growth in height is reduced, leaves become smaller and thicker, palisade tissue is very strongly developed, intercellular spaces are diminished, etc. On the other hand, certain halophytic plants (*Salicornia herbacea*, *Salsola soda*, etc.), on being transplanted into a soil with a normal content of salts, lose many of their characteristic features; they acquire, for instance, thinner leaves (Warming, 1918). Constantin proved that it was possible to impart to an organ, such as a runner or a root, a definite morphological or anatomical

structure, if it were grown at first in one medium (in the ground, for instance) and subsequently in another (say, in water). Even one and the same leaf may acquire a different structure according to the medium in which its parts grow. Thus in the water-soldier, *Stratiotes aloides*, the parts of the leaves that protrude out of the water become less transparent, get darker, acquire stomata, etc. (Constantin).

Bonnier made the following experiments. He cultivated cuttings from the same plant in low-lying ground and in the mountains, and thus succeeded in transforming *Taraxacum vulgare*, *Betonica officinalis*, *Lotus corniculatus*, *Campanula rotundifolia* in the mountains into varieties showing features of alpine plants. The terrestrial form of *Polygonum amphibium* in the course of a few months may be transformed into an aquatic one. No matter if such variations are not hereditary. "Various organs, roots, stems, leaves, hairs," says Warming (1918), "modify morphologically and anatomically in the same species, according to whether the given individual develops in water or in air, in a humid or a dry atmosphere; these very circumstances produce the structure which is in general characteristic of land or aquatic plants, or of xerophytes or hydrophytes; at least the structure of the given species is developed in that direction."

All these variations are far from being accidental. We here perceive the direct effect of the geographical landscape, and there can here be no application of the principle of infinite variability, or of the selection of the accidentally best-adapted individuals: *all* individuals of a given landscape vary in a determined direction.

Zinger (1909, pp. 188, 193) has carried out the following remarkable experiment, which has a very important bearing on the subject we are engaged in. In flax fields occurs a weed of the family Cruciferae, *Camelina linicola*, which originated, so far as is known, from the cultivated oil-seed plant, *Camelina glabrata*. This latter plant was sown in a thick growth of

flax. It then appeared that in the very first generation the vegetative organs of *C. glabrata* at once assumed all the morphological and anatomical characters typical of *C. linicola*: the *C. glabrata*, which had come up with flax had, when compared with the specimens of the same plant sown in normal conditions, thinner roots, less branching stems, thinner and longer internodes, a smaller quantity of leaves, the leaves themselves smaller, narrower and of a lighter green, a very slight pubescence on the stems and leaves, an all but complete absence of the secondary xylem, etc.—all characters typical of *C. linicola*.

To this it may be added that *Camelina linicola* is a form in which the characters of the vegetative organs are fixed by inheritance: if *C. linicola* be cultivated separately from flax, its characters remain, as far as could be traced, unchanged to the third generation (Zinger, p. 195).

6. ISLAND FORMS

Island forms are often distinguished from their continental kindred by a smaller size and darker coloration.[1] Some unaccountable law closely unites the island animals of the Mediterranean Sea in the matter of coloration, by making them darker than on the continent of Europe; they are also smaller. Thus the Corsican and Sardinian sub-species of European birds are characterised by a darker colouring and a smaller size, especially shorter wings. Such, for instance, are the endemic Corsican sub-species of the Citril finch (*Carduelis citrinella corsicana*), the common tree-creeper (*Certhia familiaris corsa*), the long-tailed tit (*Aegithalus caudatus tyrrhenicus*), the red-legged partridge (*Caccabis rufa corsa*), or the endemic Corsico-Sardinian sub-species of the raven (*Corvus corax sardus*), the hooded crow (*Corvus cornix sardonius*), the jay (*Garrulus glandarius ichnuse*), the

[1] With regard to size, the above is apparently true only of islands situated in a warmer climate than is the continent.

goldfinch (*Carduelis carduelis tschusii*), the chaffinch (*Fringilla coelebs tyrrhenica*), the rock sparrow (*Petronia petronia hellmayeri*), and many others (Jourdain, 1912, pp. 330-332). This is true not only of non-migratory Corsican birds, but likewise of some birds of passage, such as the cuckoo, nightingale, red-backed shrike. The eggs in the Corsican sub-species are smaller than in the corresponding continental species, and blue and grey prevail over red and brown ones.

Like the birds, many Corsican insects of the most diverse orders are coloured in darker hues than their continental relations (*e.g.* bumble-bees (Skorikov)). Endemic sub-species of birds of the Canary Islands are distinguished by their darker coloration (Bannerman, p. 567). The black island forms of the genus Coereba (Certhiola, sugar-bird) of the family Coerebidae, are especially remarkable. The geographical distribution of these birds is restricted to America, encompassing nearly the whole of the West Indies, and extending as far north as lat. 27° in the Bahamas. The island species of this genus are peculiar for their endemism. In some species melanism is very much developed, as, for instance, in *Coereba atrata* from St. Vincent, in *C. wellsi* from the island of Grenada, and in others. In species from various islands the black colour has been independently developed.

A genus of finches, Geospiza of the family Fringillidae, endemic in the Galapagos, contains thirty-three species and sub-species. These finches may be arranged in a series of forms exhibiting a growing tendency towards melanism. Some forms are perfectly black in both sexes and in all stages of plumage (beginning with the youngest), as, for instance, *G. conirostris* (Snodgrass and Heller, pp. 275-276).[1]

[1] Another example of melanism in the islands is afforded by the mocking birds, Nesomimus (*l.c.* p. 366). On island melanism in the wren and starling in the Faroe Islands, see Laubmann, 1915.

The mammals of the British Isles are, as a rule, darker than those of the Continent; for instance, the red deer (*Cervus elaphus scoticus*), the roebuck (*Capreolus capreolus thotti*), the wild cat (*Felis silvestris grampia*), the water vole (*Arvicola amphibius ater*) and others (*Cockerell, 1914, p. 178*).[1]

Island forms, as is known, show a tendency towards the loss or reduction of wings. This is true of beetles, flies (such as Anatalanta in Kerguelen) and birds. In New Zealand there are a number of carinate birds that have nearly lost the keel on the sternum, and thereby, as it were, approach the ratite birds; thus in the three flightless Rallidae of New Zealand, Ocydromus, Notornis (doomed to extinction), and the extinct Aptornis, the keel is very small, and it is all but absent in the ground parrot or kakapo, Stringops, and in the extinct giant goose Cnemiornis. New Zealand is also the home of true ratites, *i.e.* the kiwi (Apteryx) and the extinct moas (*Dinornithidae*).

The southern forms are frequently smaller than the northern. This is accounted for by the fact that the smaller the animal the larger is the extent of surface of the body in relation to its volume, and so a small animal loses more heat than a large one (Ramensky, 1908; Bötticher, 1915, p. 2). We have already mentioned the reduced size of the island forms of the Mediterranean in comparison with the continental forms. This fact is usually explained by the effects of insular isolation. But the influence of climate cannot be neglected. We know that in the south animals usually become smaller than in the north: this is true of hares, foxes, magpies, jays, and many fishes (chub, roach, bleak, Chondrostoma; see above, section 1); woodpeckers (Colaptes) in America become smaller as we move from North to South. Further, in *islands* situated north of Europe, birds are larger than on the continent. Thus, the wren of the Faroes, *Troglodytes troglodytes borealis* Fischer,

[1] But some (a very few) are lighter. The squirrel (*Sciurus vulgaris leucurus*) is an instance of this.

is larger than the continental *Troglodytes troglodytes* L., while the Iceland sub-species, *Tr. troglodytes islandicus* Hart., is larger still. The starling of the Faroes, *Sturnus vulgaris faroensis* Feilden, is larger than the continental form (Laubmann). Of dwarf forms from the Mediterranean islands, the fossil dwarf elephants of Malta are especially notorious. But it is easy to name many insular small forms of recent species. Such are the hedgehog of Crete, *Erinaceus nesiotes* Bate; a very small fox from Corsica and Sardinia, *Vulpes ichnusae* Miller; a badger from Crete, *Meles arcalus* Miller; a beech marten from the same island, *Martes foina bunites* Bate; the Sardinian hare, *Lepus mediterraneus* Wagner, the smallest of European hares; the Sardinian hog, *Sus meridionalis* Major, etc. (see G. Miller, 1912). The birds of Corsica and Sardinia, as we have already noted, are smaller than those of the Continent. The dragon-flies of the coasts and islands of the Mediterranean seem dwarfs in comparison with their congeners of the North of Europe. Thus, the common European *Libellula depressa* in Dalmatia, *Lestes virens* and *Sympycna fusca* in Sicily, are very small.[1]

To the same law man also is apparently subject: of all Indo-Europeans in Europe the tallest are the northerners, Scotsmen and Swedes, the shortest being the representatives of the Mediterranean race. The average height of Italians, according to Livi, is 164·5 cm.; of Southern Italians and Sardinians only 162 cm.

Marine fishes of the northern Pacific are distinguished by their large size from the representatives of the same genera and families inhabiting the North Atlantic. This is true of the Cottidae, Blenniidae and others (P. Schmidt, 1904). The same applies to the Japanese representatives of dragon-flies, as, for instance, *Calopteryx virgo* and *Anax parthenope*. Northern Foraminifera are usually larger than the southern forms; *Miliolina tricarinata* from the North Atlantic attains

[1] The same law apparently holds good with plants also; in Corsica is found a small variety of the spurry *Spergula arvensis gracilis* Pet.

the length of 5 mm., while its size seldom surpasses 1 mm. in the Mediterranean (Rhumbler, 1911, p. 200).

Many organisms dwelling in Lake Baikal are notable for their large size—Diatomeae, Planariae, Gammaridae, certain fishes (of the family Cottocomephoridae).

The theory of *the geographical landscape,* exposed above, as a formative agency in the organic world, is nothing but a further development of the ideas of those evolutionists who, following M. Wagner (1868, reprinted in 1889, pp. 64, 97 and elsewhere), insist upon the importance of *isolation.*[1]

Geographical isolation is one of the most important agencies in the creation of new forms.[2] The deeper we penetrate into the study of the geographical distribution of organisms, the more clearly do we perceive that every geographically isolated region or landscape possesses its own animals and plants. The differences between the maternal species and the form which has separated itself therefrom through the influence of new geographical conditions are greater the longer the period of isolation has been, and the more peculiar the new geographical landscape (environment) is.

Geographical isolation is realised through the adaptation of organisms (1) to the *physical environment,* namely to the land, rivers and lakes, the sea, the substratum of soil, the climate and height zones, and (2) to the *biological environment.* This latter operates in various ways, according to whether the objects acted upon are combined in a social organization (*e.g.* forest associations, migratory fishes such as the Caspian vobla, sturgeons, salmon, etc., termites, ants, bees and man), or live in solitude.

The geographical landscape thus acts in a determined direction simultaneously affecting all the organisms subject

[1] I think it necessary to state that, with E. von Hartmann (1906, p. 5) and Wettstein (1898, p. 39), I regard the *migratory* theory of Wagner as unsatisfactory.

[2] This idea is well expressed by Racovitsa (1912, p. 208) in his very pithy definition of the species, "une colonie isolée de consanguins."

to it. With such a position it is interesting to compare what Darwin says in chap. xi of his "Origin of Species" p. 291), "... our theory includes no fixed law of development, causing all the inhabitants of an area to change abruptly, or simultaneously, or to an equal degree."

CHAPTER VII

CONVERGENCE OF EXTERNAL CHARACTERS DUE TO ADAPTATION TO SPECIAL CONDITIONS OF LIFE

In Chapter V. the cases of convergence inherent in the organism, and in Chapter VI. those imposed on it by the landscape, have been considered. It remains to examine the cases of convergence which are due to a specialised mode of life. We shall confine ourselves to a few examples, as this subject is not a new one (some of the cases illustrated in Chapter V. may possibly belong here).

1. ANIMALS

The exceptional length of the first toe (hallux) is characteristic of man. Among other mammals, in the bear alone is there any similarity to the human mode of progression (apes, walking on their hind-limbs, use their arms for balancing themselves and for support). Now, we see that in the bear the hallux is lengthened (although in a less degree than in man) and lies close to the other toes.

The Marsupialia are divided into a series of families, which externally recall some of the placental families. Petaurus of the Phalangeridae, inhabiting Australia and New Guinea, very much resembles the rodent Pteromys (flying squirrel) of the Sciuridae. By the way, we may remark that the flying membrane in three genera of the Phalangeridae, Petaurus, Petauroides and Acrobates, has

developed independently. The Australian pouched banded anteater Myrmecobius of the Myrmecobiidae, is like the true American anteaters of the Myrmecophagidae belonging to the Edentata (Xenarthra).

The Australian marsupial mole *Notoryctes typhlops* (fam. Notoryctidae) in the shape of the body copies, as it were, the common mole Talpa, of the Insectivora; it still more resembles a South African insectivore, the golden mole Chrysochloris (fam. Chrysochloridae); this resemblance goes so far that even Cope was inclined to admit this to be a case not of convergence, but of consanguinity. Such a suggestion is, of course, erroneous.

According to the researches of Carlson (1904), the following points of resemblance between Notoryctes and Chrysochloris may be observed. In both the fur is thick and soft, with a metallic lustre varying between golden green and copper red; rudimentary eyes are concealed beneath the skin; the auditory pinna is deficient. There is the same peculiar position of the extremities; the paroccipital and postorbital processes are wanting; the cranial sutures are obliterated early; the bulla ossea is strongly developed; the presternum has a ridge; the first rib is strongly developed; there are many common features in the skeleton of the carpus and tarsus, as also in the musculature of the extremities, etc. The structure of the hair of the marsupial mole in every detail corresponds to that of the common mole (Friedenthal, 1909). In Notoryctes, in addition, many features of resemblance to the armadillos (Dasypodidae, of the Edentata) are to be observed.

Among the Marsupialia we further find in the Peramelidae analogues to the Insectivora, in the Dasyuridae to the Carnivora, Rodentia and Insectivora; thus, the representatives of the genus Dasyurus in their outward appearance and habits recall martens; the pouched jerboa Antechinomys resembles the jerboa; Sminthopsis resembles the shrew, even in the structure of its hair. The Tasmanian wolf (*Thylacinus cynocephalus*) is externally very like a small

wolf; this similarity extends to the skull, which, while of course preserving the typical features of a marsupial, much resembles that of a dog.[1] The marsupial bones in this genus are reduced. The koala or Australian bear (*Phascolarctos cinereus*) is very much like a true bear.

The similarity between the large South American rodent Dolichotis, belonging to the family of guinea-pigs, Caviidae, and the South American deer Pudua, belonging to the Cervidae and extending northward into Mexico, is remarkable.

Many rodents display a similarity to insectivores: mice very much resemble shrews (Crocidura), and porcupines (Hystricidae) hedgehogs (Erinaceus). Squirrels (Sciuridae) inhabiting India and the Malay Archipelago, very much recall insectivores of the family Tupaiidae. Both live in trees and much resemble each other in size, external appearance (in the shape of the tail, etc.) and habits. Thus the squirrel *Rhinosciurus tupaioides* is very similar to *Tupaia ferruginea*; this resemblance extends to the coloration and even to the white shoulder stripe and the elongated muzzle. Wallace even saw in the tupaias evidences of mimicry, the only case among mammals. The flying lemur (Galeopithecus), distributed in Indo-China, in the Malay Archipelago and the Philippine Islands (a representative of a distinct order, the Dermoptera, closely allied to the Insectivora), resembles the flying squirrel Pteromys of the Sciuridae. This animal was formerly referred either to the Chiroptera or to the lemurs. It is close to the stem which gave origin to the Insectivora, and is not far removed from the bats, but undoubtedly represents an independent branch (M. Weber, p. 411).

The Cetacea and Sirenia (manatees, dugongs and sea-cows) belong to two different orders, having essentially nothing in common. The whales form a very aberrant

[1] This similarity is also recorded by Darwin ("Origin of Species," chap. xiv, p. 374).

group, whose affinities are not clear. The herbivorous Sirenia are not very distantly allied to the ungulates. Regardless of the fact that anatomically both groups are very far apart, their structure nevertheless reveals a series of similar features: a fusiform body, absence of hinder extremities, transformation of the fore-limbs into flippers, presence of a caudal fin, the structure of the labyrinth, the elongation of the lungs and their transformation into a kind of an hydrostatic organ, the disappearance of hairs and of the external ear.

The whale, *Balaena glacialis*, in its habits, bipolar geographical distribution and external form, recalls the giant basking shark of northern waters, *Cetorhinus maximus* (or (*Selache maxima*). Both are of enormous size, and possess a blunt snout, large mouth, small eyes, diminutive brain; both feed on plankton.

A diprotodont dentition, in which the anterior pair of teeth are transformed into prominent incisors, occurs in the most diverse orders of mammals, such as the Insectivora, Rodentia, Simiae, Tillodontia (fossil Eocene Placentalia of North America, in some respects similar to rodents), primitive Edentata and others (Osborn, 1910, p. 11).

A transformation of the hind-limbs into organs for leaping occurs in the jerboas (Dipodidae), in the South African Cape jumping hare Pedetes (Pedetidae, Rodentia), in American rodents of the family Heteromyidae, in the African jumping shrews (Macroscelidae, Insectivora), in Marsupialia (kangaroos), etc.[1]

In the forests bordering the middle Amazon occur small nocturnal monkeys of the genus Nyctipithecus (Douroucoli). In the day-time they sleep in the hollows of trees, and come forth to prey on insects and eat fruits only in the night. Their body is 30 cm. long, the tail being somewhat longer. "Their physiognomy," says Bates (chap. xii, p. 333), "reminds one of the owl or tiger-cat: the face is round and

[1] For a fuller treatment of the subject see Abel, 1912, p. 257 *seq.*

encircled by a ruff of whitish fur; the muzzle is not at all prominent: the mouth and chin are small; the ears are very short, scarcely appearing above the hair of the head; and the eyes are large and yellowish in colour, imparting the staring expression of nocturnal animals of prey. The forehead is whitish, and decorated with three black stripes."

In the forests of South and Central America (and partly in the West Indies) may be found mammals with prehensile tails, belonging to various orders: besides the universally known monkeys, to which the above-mentioned Nyctipithecus is referred, we may mention the kinkajou, Cercoleptes, very much resembling a lemur (the Indians on the Amazon regard it as a monkey), but belonging to the Procyonidae, which are allied to the bears; the wonderful tree-porcupines (fam. Cercolabidae) Cercolabes; and Chaetomys, a prehensile-tailed rodent, *Capromys prehensilis*, of the Coypu family (Octodontidae); the little arboreal anteater, Cycloturus, of the Myrmecophagidae; and, finally, the marsupials Didelphys and Caenolestes.

In the Falconidae those species which catch their prey on the wing have wings resembling those of the swift or the humming-bird in shape and structure; they are long and pointed, the elongation being solely due to the considerable length of the primaries, the skeleton itself being short (Suschkin, 1902, p. 378).

In Suschkin's opinion (1902, p. 387), the families of the Falconidae and Aquilidae, of which the first is the more specialised, are derived from a common ancestor. In Micrastur of the Falconidae (sub-fam. Herpetotherinae), owing to its being adapted to the pursuit of prey in dense forests, a striking likeness to hawks (fam. Aquilidae) is manifested. Other forms of Aquilidae, such as Thrasaëtus and Morphnus, very far removed from hawks, dwelling in thick forests, acquire the outward appearance of hawks. The caracaras (sub-fam. Polyborinae, fam. Falconidae), a Neotropical group of falcons, bear a general resemblance to

those representatives of the Aquilidae which subsist on similar food (*carrion*). In particular, Suschkin (1902, pp. 389-390) notes the widened gape in the higher caracaras, and in consequence a modification in the position of the axis of the quadrate. The same feature may be observed in many *Aquilidae that live on carrion: in vultures and* Haliëtus. "In this instance we see a contrivance for swallowing large mouthfuls." A spoon-like depression in the palatal surface of the maxilla in Polyborus, and also in Gyps and Pseudogyps, *may further be noted.*

The worm-like subterranean lizards of the family Amphisbaenidae show a resemblance to Coeciliae, limbless Amphibia (Gymnophiona or Apoda) leading a similar mode of life. In the limbless Amphisbaena the tail is rudimentary, and the vent is situated almost at the extremity of the body; the eyes are concealed under the skin; the skin is soft, constricted into rings, deprived of scales; the skull is compact. All these features are shared by the Coeciliae (Gymnophiona), some of which, such as Typhlonectes, are likewise devoid of scales. Owing to the ring-shaped constrictions of the skin, progression both in the Amphisbaenidae and the Coeciliae is effected by the peristaltic motion of the body, as in earthworms (*Lumbricidae*). Rhineura, a blind amphisbaenian lizard, abundant in some parts of Florida, in shape, colour, annular arrangement of its dermal plates and vermiform progression strikingly resembles an earth-worm.

Snakes of the families Typhlopidae and Uropeltidae, leading a subterranean life, also very much resemble Gymnophiona.

Two fishes, Anableps and Dialommus, inhabiting Central American waters, as we have already had occasion to mention, have peculiarly constructed eyes, which do not recur in any other vertebrates: the cornea is divided by a horizontal band into two portions, the upper and the lower, enabling these fishes simultaneously to see in the air with the upper portion and in the water with the lower. But it is

noteworthy that both genera belong to two distinct orders: Anableps is a fresh-water fish of the order Cyprinodontiformes (family Cyprinodontidae), and Dialommus, a marine fish of the Panama Coast is a member of the order Perciformes (fam. Blenniidae).

In the so-called telescopic eyes of deep-sea fishes occurs a supplementary retina, the function of which has not as yet been incontrovertibly ascertained. A similar structure is found in the telescopic eyes of certain Crustacea (Cladocera, Schizopoda), insects (may-flies, dragon-flies, Diptera [1]); something of the kind is observed in heteropodous Mollusca, in the wasp Vespa, in the slug Limax, in the worm Alciope (Brauer, 1908, p. 240 *seq.*).

South American siluroid fishes of the family Loricariidae, especially *Loricaria* (*Sturiosoma*) *rostrata*, remarkably resemble the Mississippi and Turkestan shovel-nosed sturgeons (Scaphirhynchus), which belong to an entirely different group, the Acipenseridae. (These are Chondrostei, whereas the siluroids are teleostean fishes.) Both species inhabit the bottom, feeding on the denizens of the river mud. In both, the hind part of the body is covered with an armature of bony plates, the snout is elongated and shaped like a spade, the eyes are small, the mouth is inferior, the lobe of the caudal fin is produced into a long, thread-like appendage, the caudal vertebrae are depressed as in *Scaphirhynchus platyrhynchus* (Berg, 1905, p. 26).

The Nototheniidae, a family of Antarctic fishes, in their different representatives remind one very much of the Cottidae, which not only belong to a distinct order, but are peculiar to the Northern Hemisphere. In the mountain streams of Central Asia the Salmonidae are replaced by the so-called "split-bellied" Cyprinidae (Schizothorax, Diptychus

[1] G. Shafer ("Proc. Wash. Acad. Science," viii, 1907) has studied the divided eyes in certain Odonata and Diptera. He thinks that the divisions of the eye are for vision in different kinds of light, the regions with larger elements and less dense pigmentation being available in twilight or in the darker hours.

and others), some of which closely resemble salmon in the shape of the body, scales, coloration and habits.

Such "imitators" very frequently occur amongst the South American fishes of the group Characinoidei.

> The small *Poecilocharax bovalii* from British Guiana so much resembles the killifishes (Cyprinodontidae, or Poeciliidae) that Eigenmann, the leading authority on the Characinoidei, *referred this genus to the latter not* without hesitation.[1] The representatives of the genus Characidium, which live in sand shoals or amongst the rocks of rapids, are very like the North American Percidae of the Etheostomatini group, which lead a similar life. *Characidium vintoni* is like Hadropterus, *Ch. blennioides* is like *Etheostoma coeruleum*, *Ch. pellucidum* (as also *Ch. pteroides*, *Ch. catenatum*) resembles *Ammocrypta pellucida*. (See Eigenmann, 1912, p. 288 *sq.*) *Luciocharax insculptus* is a garpike-like characin; *Salminus affinis* resembles a salmon; *Prochilodus longirostris* is like a sucker (Catostomidae); *Chalcinus magdaleneae* is practically a herring. But the Characinoidei imitate not only representatives of other groups of fishes, but their own kin. Thus the Guiana *Moenkhausia lepidura* of the Tetragonopterus group very much resembles another fish of the same group, *Creatochanes caudomaculatus*, which is not infrequently seen in company with it; the fry of *Anostomus anostomus* is indistinguishable from that of *Leporinus arcus* (Eigenmann, 1912, p. 112).

G. G. Jacobson has communicated to me the following facts concerning the distribution of the beetles of the sub-family Carabini. The genus Carabus nowhere breaks the bounds of the Palaearctic region in the Old World, while Calosoma has a much wider distribution. Now, in the Abyssinian mountains and Kilimanjaro, where the genus Carabus is absent, Calosoma acquires its outward aspect. (Jacobson has described a wingless Calosoma from Galaland under the name of Carabops.) In the mountains of Mexico representatives of Calosoma very much recall Carabus.

In North-western Tibet occur two ground-beetles, *Carabus*

[1] Eigenmann, 1912, p. 112, pl. xliv, f. 1, 2.

(*Carabus*) *roborowskii* and *C.* (*Rhigocarabus*) *morawitzianus*, which, in spite of their belonging to two distinct subgenera, are so similar that the well-known entomologist Morawitz regarded them as representatives of one species (Semenov, 1900, pp. 624-625).

The Brazilian bug Ghilianella (Reduviidae) very much resembles a young Mantis: it has a stick-shaped body and extremely long and thin legs, like those of a daddy-long-legs (Tipulidae). In another bug, belonging to the same family, *Ploearia pallida*, inhabiting Woodlark Island, the legs, as in the Tipulidae, are also very long and thin; and here again, as in the Diptera just named, they are coloured in alternate bands of black and white.

The Californian wingless scorpion-fly, *Bittacus apterus* (Panorpidae, order Mecoptera), pursues daddy-long-legs, which it very much resembles in outward appearance.

The larvae of Trichoptera of the genus Helicopsyche construct spiral cases of pebbles and sand, wonderfully resembling shells of Mollusca. The larvae of some golden-eyes or lace-wing flies (Chrysopa, Neuroptera) bear a general resemblance to those of lady-birds, and, what is remarkable, hunt their victims after the same fashion. The aquatic caterpillar of the moth *Cataclysta lemnata* (Europe) constructs its dwelling or case of duckweed (Lemna) or of pieces of reed 3-4 cm. long. These cases very much resemble those of the larvae of the caddisfly Agrypnia, inhabiting the same waters and constructing its case of the same reeds.

Insects living in the hair, wool and fur of mammals are wingless, have an elongated body tapering in front, and a depressed head; the margins of the body and head have no projections. Such are flies of the families Streblidae and Nycterebiidae, living as parasites on bats. Such also is the beetle *Platypsyllus castoris* living on the beaver. Such, lastly, are the singular bugs Polyctenidae, parasitic on bats, and long held to be flies of the family Nycterebiidae or bird-

lice (Mallophaga). These bugs are very small insects, 2½-4 mm. long, the ten species of which inhabit the tropics. They alone among bugs are viviparous, and constitute a family, closely allied to the Cimicidae, to which the common bed-bug belongs (Horwath, 1911).

It is remarkable that both in the bugs Polyctenidae and the flies Streblidae the head is divided into two parts : (1) a terminal, crescent-shape, movable section, and (2) a basal section. The two are united by an articulation. The Polyctenidae, like very many parasites, are destitute of eyes. In the Old World species a peculiar modification of the claws is observed, which occurs also in horse-flies (Hippoboscidae). The tibia in Polyctenidae has light-coloured rings ; similar rings occur in some Nycterebiidae, which, as we have said, are likewise parasitic on bats. In Polyctenidae we may further observe a structure quite unknown in all other bugs, *i.e.* combs consisting of a series of spines on certain parts of the body. Such combs frequently occur in insects living on the hair of mammals, *e.g.* in fleas, Nycterebiidae, certain Streblidae, Platypsyllus, in the beetle *Silphopsyllus desmanae* (Olsujev, 1919), living on the Russian desman Myogale, etc. They serve for attaching the insect to the hair.

Everyone knows the so-called "claws" (chelae) of scorpions and of other orders of the class Arachnida on the one hand, and of decapod Crustacea on the other ; but Kirichenko has drawn my attention to the fact that also in certain bugs (Carcinocoris, Carcinochelis) belonging to the Phymatidae, distributed in India and Indo-China, the anterior pair of legs are transformed into chelae (Handlirsch, 1897, pp. 219-221, Taf. VI, Figs. 1-3). Peculiar extremities resembling a clasp- or pocket-knife have developed independently in Squilla (Stomatopoda, of the class Crustacea), the mantis and the Mantispidae (Neuroptera) ; Jacobson has pointed out to me that the same type of extremities occurs in the fly *Ochthera mantis.*

The siliceous skeleton of certain Heliozoa is very similar to that of the Radiolaria.

Convergence, due to adaptation to a specialised mode of life, may also affect *psychical* phenomena. In this connection we may mention points of similarity in the habits and instincts which have been quite independently evolved in social animals, such as the termites, ants, bees, wasps and man. A remarkable case of psychical convergence is manifested in termites and ants belonging, as is well known, to perfectly distinct orders. The similarity in this case extends to details. The "fungus nurseries" which are cultivated by South American ants (Atta and others) are universally known. Exactly similar nurseries have been found in the nests of African termites. For cultivating the fungus the Atta ants ascend trees to cut off the leaves and return with them to their nest. The same act is performed by termites. The latter, like ants, march in columns attended by "soldiers." The very method of cutting and carrying the leaves is identical in both (Escherich, 1908). The association of insects with fungi, independently evolved in various groups also occurs in some wood-boring beetles (Xyleborus, Xyloteres) and in flies producing galls (Cecidomyidae). (See Neger, 1913, p. 503 *seq.*)

Willey (1911, pp. 131-132) gives yet another illustration: the males of the siluroid fish Arius and of the South American toad *Rhinoderma darwini* both hatch their young in their mouth.[1]

2. PLANTS

American cactuses, many African Euphorbiaceae and South African Stapeliae, belonging to three families far removed from one another in the system, exhibit a very similar and at the same time peculiar outward appearance, which is due to adaptation to definite external conditions.

[1] On the oral gestation in the North American catfish *Felichthys felis*, see Gudger (1918).

The same is true of some water plants, such as Nymphaeaceae, Limnanthemum of the Gentianaceae and Hydrocharis of the Hydrocharitaceae, which strikingly resemble one another.

Tillandsia usneoides (fam. Bromeliaceae), an American flowering plant-like lichen, thickly covering tree trunks, very much resembles the common lichen *Usnea barbata*. The American parasitic flowering plant *Scybalium fungiforme* (fam. *Balanophoraceae*) externally bears an unusual resemblance to a fungus. In the parasitic *Rafflesia arnoldi* (Sumatra) the stem, leaves and roots are represented by thin filaments, recalling the mycelium of fungi (when in bloom Rafflesia produces flowers one metre and a half in diameter). Aquatic dicotyledons belonging to the family of Podostemaceae (order Rosales) and living in rapidly-moving water, both in external form and internal structure simulate algae (*e.g.* Fucus), liverworts, mosses, and lichens. Thus *Podostemon olivaceum*, growing in South America on rocks in waterfalls, looks like the thallus of a liverwort (D. Scott, 1911). *Bostrychia moritziana*, a fresh-water alga of the family Florideae, "in its morphological construction is closely analogous to *Podostemon subulatum*, and also occurs in the rapids of the mountain streams of Guiana, occupying there the same localities as the Podostemacea, *Oenone imthurni*" (Willis, 1902, p. 420; cf. also p. 331). The Tristicheae, one of the least modified groups of the Podostemaceae, presents remarkable similarities in morphological features and in the arrangement and anatomy of the leaves, to many mosses and liverworts (Willis, p. 421).

The leaves of the Cordaites (a group akin to Coniferae) possess the same contrivances for withstanding the effects of wind as recent monocotyledons display: in both the leaf is supplied with parallel veins of dense fibrous tissue on its upper and lower surface (Scott).

The convolvulaceous Cuscuta, deprived of chlorophyll, resembles another plant, also parasitic, the lauraceous

Cassytha (Neger, pp. 137-138). No less remarkable in adaptation to aquatic life are analogous modifications to which the leaves of plants belonging to various families are subject: the submerged leaves are deeply dissected and become thread-like in shape, as in *Myriophyllum elatinoides* (Haloragaceae), *Hottonia palustris* (Primulaceae), Utricularia (Lentibulariaceae), *Ranunculus fluitans* and *R. aquatilis*, the American *Cabomba aquatica* (Nymphaeaceae) and many others. Some have both submerged dissected and floating entire leaves (as, for instance, the above-mentioned Ranunculi and Cabomba) (Neger, p. 261).

The Casuarinaceae, trees or shrubs, chiefly distributed in Australia and the Malay Archipelago, bear a resemblance to horse-tails and to the gymnosperm Ephedra. The thin branches of the Casuarinaceae, just as in horse-tails, rise from the axils of small scaly leaves, which usually fuse into a dentate sheath. The internodes are long, jointed, easily breaking up into separate pieces, as in horse-tails, and, like these, are for the most part supplied on the surface with longitudinal, projecting ribs. And yet the Casuarinaceae have nothing in common with horse-tails; they are primitive flowering plants, possessing two cotyledons and occupying the lowest position in the group of the Monochlamydeae (see p. 211).

Many more cases of convergence due to adaptation to a similar kind of life could be presented. This very widely-spread phenomenon is, undoubtedly, strictly subject to some laws, being unaffected by natural selection.

CHAPTER VIII

MIMICRY AND RELATED PHENOMENA

1. MIMICRY.

> Natural selection is a real factor in connection with mimicry, but its function is to conserve and render preponderant an already existing likeness, not to build up that likeness through the accumulation of small variations, as is so generally assumed.
> PUNNETT, *1915*, p. *152*.

BY "mimicry" many things are meant, and we shall therefore give a definition of that term.

Mimicry, as distinguished from protective coloration and resemblance, may be defined as follows. Certain inoffensive animals externally resemble others, inhabiting the same locality, which are invulnerable from the attacks of enemies by possessing poisonous or stinging organs or some other means of defence.[1]

Thus, for instance, *Hierococcyx varius*, an Indian cuckoo, in shape and colouring so much resembles the Indian hawk *Nisus badius* that many small birds are deceived thereby.[2] Some staphyline beetles with short elytra, dwelling in the nests of ants, externally very much resemble their hosts. Flies of the genus Volucella, which lay their eggs in the nests of bumble-bees, are extremely like the latter, etc.

[1] Jacobi, 1913, p. 64. The author of this most recent and valuable monograph on mimicry shares the generally accepted view on the subject. The excellent book on mimicry written by Punnett (1915) became known to me only after the Russian edition of "Nomogenesis" had been issued.

[2] The common European cuckoo, *Cuculus canorus*, is also like a hawk, whence the Russian proverb, "To exchange a cuckoo for a hawk." On mimicry in birds, see R. Sharpe.

The origin of such imitative acts affecting forms and coloration is usually accounted for in the following manner. Accidental variations leading in the direction of copying the model were useful for the inoffensive imitators, and were therefore permanently fixed by selection. But such a concurrence of accidents is quite improbable. A coincidence in the concurrence of accidents is still more so. Thus, the flies of the genus Volucella, just mentioned, occur also in the New World. And yet both in the Old World and in the New they imitate the bumble-bees.[1] The species *Volucella bombylans*, further, falls into several sub-species, each of which imitates its species of Bombus. Is an *accidental* occurrence of the features of Bombus in these flies conceivable ? It would be quite as probable as the supposition that a word, say "Washington," could be obtained by picking out at random letters from a heap containing the whole alphabet. It is obvious that in many species of Volucella, under the effect of causes hitherto unascertained (see below), a general tendency towards evolution in the direction of the external forms of Bombus is displayed.[2]

Besides the above, we may present the following arguments as a refutation of the current theory of mimicry.

(1) As a rule, the imitated and the imitator live side by side. According to Wallace ("Darwinism," 1889), this juxtaposition is an essential condition for the occurrence of mimicry. Many cases, however, are known in which the two inhabit different continents. For example, one African wagtail, *Macronyx croceus*, "mimics" the North American troupial *Sturnella magna* (troupials belong to the Icteridae, a family

[1] R. Pocock (1911, p. 847) gave *Volucella bombylans* as food to various birds in the Zoological Gardens in London, but the latter either refused to eat the flies or did so as if unwilling. If it be true that the fly is not consumed by birds, mimicry in this case would defeat its object. Pocock, however, suggests that it may be a case of the so-called Müllerian mimicry (for which see below).

[2] We may remark that certain species of Volucella do not imitate bumble bees. And it should be noted that one species of the genus Mesembrina (Diptera) living on excrements is like a Bombus, while the other is not.

replacing in the New World starlings and orioles), while another African species, *Macronyx ameliae*, very much resembles in coloration the South American *Sturnella defilippii*.[1] Another American troupial, the red-winged blackbird, Agelaeus, "mimics" the African shirk, *Camephaga phoenica*. Other troupials of the genus Icterus, coloured black and yellow, very much resemble orioles; yet there are no orioles in the New World, neither are there troupials in the Old. The New Zealand cuckoo, *Urodynamis taitensis*, very much resembles the North American hawk, *Accipiter cooperi*.[2]

In the forests of the Argentine, near Palermo, two butterflies occurring in close proximity are met with, one of which strikingly recalls the European *Vanessa* (*Araschnia*) *prorsa* in coloration and manner of flight, while the other resembles the form *levana* of the same species. Nor is that all; for an angular projection on the fore-wings of *V. prorsa* is repeated in a corresponding position in the Argentine butterfly. And yet the genus of that American butterfly, Phyciodes, is not even related to the European one. "Had both genera occurred together in our part of the world," says Seitz (p. 319), "no one would hesitate to regard the resemblance as a typical case of mimicry."

The African butterfly *Charaxes brutus*, belonging to the family of Nymphalidae, very much resembles the Brazilian butterfly *Dasyophthalma rufina* (fam. Brassolidae) in colour and pattern. The similarity between *Limenitis zayla* from Sikkim and *Adelpha erotia* from South America (as also *Apatura lukasi* from the same continent) is remarkable; all three are Nymphalidae (Eimer, 1897, p. 140, Figs. 66, 67). Two nymphalid butterflies, *Rhinopalpa sabina* from Java and *Palla decius* from the Gold Coast of Africa, are alike in size, shape and coloration (*l.c.*).

An African species of wasps of the genus Bembex and a South African genus of the same insects, Monedula, are extremely like one another.

[1] Keeler, pp. 239-240. [2] Menzbier, pp. 141, 142.

South American acridiid locusts, Proscopiidae, can hardly be distinguished from certain stick insects (Phasmatodea), although hitherto Proscopiidae and stick insects have never been met with together (we may add, that Proscopia is wonderfully like the dried grass-stems among which it lives). In this case it is obvious that the similarity between the locust and the stick insect is due to the tendency of both to vary in one similar definite direction. Such a tendency is aboriginal, and natural selection is powerless in this matter to effect anything.

Since the days of Wallace ("The Papilionidae of the Malayan Region," 1865), the case of the butterfly *Papilio polytes*, very common in India and Ceylon, is given as a classical instance of mimicry. This species has three forms of females: (1) resembling the male, (2) resembling *Papilio aristolochiae*, and (3) resembling *P. hector*. Both *P. aristolochiae* and *P. hector* are considered to be inedible. Yet Punnett (1911, pp. 8, 9; compare also Punnett, 1915, chap. vii) has observed in Ceylon that high in the mountains *P. hector* becomes rare and *P. aristolochiae* very abundant, while the female of *P. polytes* which mimics *P. hector*, is more abundant than that which mimics *P. aristolochiae*. In the north-east of Ceylon, on the contrary, the imitator of *P. aristolochiae* is quite as frequent as that of *P. hector*, although *P. aristolochiae* itself is here very rare; on the other hand, in Peradeniya (also in Ceylon), where *P. aristolochiae* is very abundant, its imitator is very rare. These facts are inconsistent with the generally accepted theory of mimicry: there is no sense in mimicking butterflies, which are so rare in a given locality that they are met with much less frequently than the imitators. Why, asks Punnett, should the imitator of *P. aristolochiae* be more abundant in those places where the imitated form is nearly absent, and rare where the *P. aristolochiae* is numerous?

Fryer (1914, p. 235) has recently made experiments on the crossing of the various forms of the females of *P. polytes*. It

appears that the eggs of the female resembling the male produced, in addition to males (which are all of one type and do not concern us here), either (1) the same kind of females, or (2) the same kind of females and mimicking females in equal number, or else (3) mimicking females alone. The eggs of the female mimicking *P. aristolochiae* produced females (1) resembling the male and mimicking in equal numbers, or (2) resembling the male and mimicking in the proportion of 1 to 3; or else (3) mimicking forms only. Out of the eggs of females resembling *P. hector* females were hatched either (1) resembling the male and mimicking in equal numbers, or (2) resembling the male and mimicking in the proportion of 1 to 3, or else (3) mimics only. Evidently we have here a segregation of characters according to the type of Mendelian inheritance. Of the two pairs of factors *Aa* and *Bb*, *A* is the factor causing the female to mimic *P. aristolochiae*, *B* the factor operating only in the presence of *A*, and in that case causing the imitation of *P. hector*. There are thus nine genotypic forms of males (of which only one is phenotypic) and nine genotypic forms of females (of which only three are phenotypic):[1]

Males.	Females resembling males.	Females resembling *P. aristolochiae*.	Females resembling *P. hector*.
aaBB	*aaBB*	*AAbb*	*AABB*
aaBb	*aaBb*	*Aabb*	*AaBB*
aabb	*aabb*	—	*AABb*
AaBB	—	—	*AaBb*
AaBb	—	—	—
Aabb	—	—	—
AABB	—	—	—
AABb	—	—	—
AAbb	—	—	—

Punnett has pointed out (1915, p. 92), and in this matter Goldschmidt (1920) is in perfect agreement with him, that

[1] The terms are borrowed from Goldschmidt, 1920, p. 358.

there can be no question in this case of the influence of natural selection: the factors determining the resemblance to *P. aristolochiae* and to *P. hector* are also possessed by the male, but in him they are not displayed. It is obvious that the phenomena of mimicry are generally referable to such a type: combination of factors that had earlier been present in the group to which both the imitator and the imitated belong, are alone manifested.

2. As a general rule, similarity may be explained by natural selection, only if it be useful. But we know many cases of entirely useless mimicry.

The question as to whether birds do actually eat butterflies or not, was long debated. The remains of butterflies are very rarely found in the intestines of birds; M'Atee says that of 48,000 birds' stomachs examined in the United States, only five were found to contain remains of butterflies. This gave the opponents of the theory of mimicry grounds for asserting that butterflies are never hunted by birds. Eimer (1897, p. 274) maintained that the extermination of butterflies by birds is very much exaggerated. He quotes Pipers, who only four times witnessed the persecution of butterflies by birds during his twenty-eight years' residence in the Malay Archipelago. But the inferenee proved to be incorrect. G. Bryan witnessed an *Euphagus cyanocephalus* (Icteridae) in California consuming *Eugonia californica* (Nymphalidae) in vast numbers. Manders (1911), through observation and experiments conducted in natural surroundings in India and Ceylon, concluded that birds exterminate butterflies to a much greater degree than was previously supposed; according to his computations (p. 741), one hundred bee-eaters (Merops) could exterminate all the butterflies of one species (*Catopsilia pyranthe*) on a forest road of about seventy miles long within a period of two weeks. But it is noteworthy that birds, in India and Ceylon at least, make no difference between "edible" and "inedible" species: with equal satisfaction they consume both the "unpalatable"

Danais and *Euploea*, which are the imitated forms, and the "savoury" *Hypolimnas* and *Papilio*, which mimic them so unsuccessfully. So that all this masquerade is to no purpose. No insectivorous bird in Ceylon exhibits a preference for some one kind of butterflies before any other: all butterflies are equally acceptable to it. Moreover, with all the similarity of some imitators to their models, as, for instance, of the female *Hypolimnas misippus* to *Danais chrysippus*, they are not difficult to distinguish on the wing, as Hypolimnas flies near the ground, while *Danais chrysippus* flies at a greater altitude.[1] To distinguish *Prioneris sita* (imitator) in flight from *Delias eucharis* is still easier. Therefore Manders supposes that after a little experience birds may be very easily taught to distinguish the inedible "models" from the imitators which are good to eat. But this is not all. It appears that the "inedible" butterflies Danais and Euploea, most frequently serving as objects for imitation, *i.e.* which are best protected, become the prey of birds owing to their common occurrence and confidence more often than the representatives of any other group.[2] Thus it would be perfectly useless to mimic them. The same, with respect to Ceylon, is confirmed by Fryer (1911, p. 618): the wood-swallow (*Artamus fuscus*) specially hunts after Danais and Euploea, as they fly so much lower than others. The mimicry by the female *Papilio polytes* Fryer (1914, p. 250) considers to be useless to that insect.

The diminutive moth, *Tinea pronubella*, in colour and pattern "mimics" the large moth *Agrotis pronuba* (Eimer, 1897, p. 265), which is obviously but another case of perfectly useless mimicry.

In some butterflies only one pair of wings "mimics" the wings of another species. In others, only the upper surface

[1] Manders, p. 703. But when not on the wing they can be easily mistaken for one another, and even the male *H. misippus* not infrequently takes *D. chrysippus* for a female of its own species (*l.c.*).

[2] Among birds the drongo, Dicrurus, exterminates quantities of butterflies (Danais, Euploea, Hypolimnas and other). See Manders, p. 725.

of the wing is subject to mimicry; thus the female of *Paleronia ceylonica* (Pieridae) with outspread wings very much resembles *Danais vulgaris* (Danaidae) and other species of the same genus; but on the wing they are entirely different, as the coloration of the lower surface of the wings is not the same (Punnett, 1911, p. 2, Pl. II, Figs. 1, 2). Besides that, the "model" and the "copy" may very often be distinguished at once by the character of their flight—as *Papilio clytia* var. *dissimilis* from species of the genus Danais, or *Papilio polytes* and its polymorphous females from *P. hector* and *P. aristolochiae* (Punnett, 1911, pp. 2, 8).

Can it be seriously thought for one moment that an ant falls victim to a delusion, like little Red Riding Hood, and takes a staphylinid beetle (as, for instance, Dinarda) inhabiting its nest for its own kin? Let us recall the experiment of Darwin. "Several times," he says ("Variation of Animals and Plants," ii, chap. xxii, p. 251), "I carried ants of the same species (*Formica rufa*) from one ant-hill to another, inhabited apparently by tens of thousands of ants; but the strangers were instantly detected and killed. I then put some ants taken from a very large nest into a bottle strongly perfumed with assa-foetida, and after an interval of twenty-four hours returned them to their home; they were at once threatened by their fellows, but were soon recognised and allowed to pass. Hence each ant certainly recognises, independently of odour, its fellow." Or what possible advantage would be gained by the wingless fly Termitoxenia, inhabiting the termites' nests in India, Java, Sumatra and Africa, from its similarity to termites? Or the staphylinid beetle, Termitomimus, living in the nests of termites?

"Africa," says Punnett (1915, p. 150), "is apparently destitute of Pierids which mimic species belonging to other groups. Yet no group of butterflies is more persecuted by birds. If birds are the agents by which mimetic likenesses are built up through the cumulative selection of small

variations, how can the rarity or absence of mimetic Pierids in the Old World be accounted for ?"

Sesiid butterflies with transparent wings, occurring in our part of the world, mimic wasps (see Jacobi, pp. 86-87 on the subject). Referring to this fact, Danilewsky (pt. ii, p. 165) justly remarks that if the resemblance of the butterfly to a wasp may protect it from birds which feed on butterflies, it would afford the butterfly no help against bee-eating birds. "It matters little to the insect whether it be devoured by a butterfly-eating, or a bee-eating, bird."

3. It might be expected that only palatable butterflies would mimic unpalatable ones. As a matter of fact, not a few cases are known where inedible butterflies mimic other inedible species. Thus in four families, Danaidae, Neotropidae, Heliconidae and Acraeidae, species occur in South America which, although of an offensive taste, resemble each other in colouring and the shape of the wings.[1] It would seem that in this case the theory of mimicry is completely wrecked. Not so. Fritz Müller (1879) has suggested the following subtle explanation of the matter: birds are only taught by experience which butterflies are edible, and which are *not*; and *thus the butterflies behave on the* principle "all for one, and one for all": having found one species inedible, the young birds will leave the others in peace. This "mutual insurance company" is associated with edible species of the Pieridae, which mimic the inedible Heliconidae.[2]

But Manders, who made "Müllerian mimicry" the subject of his studies in Ceylon, exposed the illusory character of these arguments (obvious, however, though it had been from the first). As is suggested by the adherents of "Müllerian mimicry," Poulton among them, *young* birds

[1] This "circle of mimicry" may be seen in a coloured plate (ii, Figs. 12-15) in Weismann, "Lectures on the Theory of Evolution," or in a coloured plate facing p. 57 (Figs. 1-4) in "Darwin and Modern Science," Cambridge, 1909.

[2] Weismann, Figs. 16-19.

alone make experiments as to the edibility of butterflies, the adult birds having already acquired sufficient experience on that head. In Ceylon cases are known in which inedible butterflies mimic inedible ones, as is done by several species of Euploea. But in Ceylon young birds are hatched in May, June and July, and their experiments may last till October; *the flight of the Euploea butterflies continues from March* till December. Three days after its appearance the butterfly begins to lay its eggs. Therefore, even if Müller's theory be admitted to be correct, a vast number of butterflies would evade being experimented upon by the young birds, and would thus have time to lay their eggs (Manders, pp. 743-744). But, besides *this, observations have shown that* drongos (Dicrurus) and other birds feed on the inedible Euploea (and the Danais similar to them) in large quantities.

4. Many butterflies occur that are vigorously attacked by birds, and yet exhibit no tendency towards mimicry. And yet selectionists admit the occurrence of an infinite number of variations, and it is inconceivable why *Hypolimnas misippus*, for instance, should have been enabled to acquire a resemblance to a danaid butterfly, while Catopsilia, living next to it, could not do so. In reply to this it might be said that Hypolimnas was endowed with the tendency to vary in the direction of a resemblance to Danais, while Catopsilia was not. But that is just what we assert: the potential power of mimicry in some forms is present before a problematical selection can assume its sway.

5. Yet one argument remains. For those butterflies which mimic other, poisonous, butterflies, it would seem much simpler to acquire not the coloration of their "models," but their "immunity," *i.e.* the property of being poisonous. If selection had played a part in the production of forms, the probability that the body of a given organism would be endowed with poisonous ingredients is no less than that of acquiring an extremely complex pattern, in imitation of the pattern of another species.

By the *foregoing* arguments we *do not* seek to prove that mimicry is *always* useless. Our object is to demonstrate (1) that *not infrequently* the utility of mimicry is problematical, and (2) that the explanation of the *origin* of mimicry by means of the struggle for life is inadequate. But when mimicry has arisen, it may, of course, be beneficial to the organism.

2. AN ANALOGOUS PHENOMENON IN PLANTS

The following phenomenon in the vegetable world may be regarded as holding a position parallel with mimicry.

Flax-fields are regularly obstructed by a number of species of plants which do not otherwise occur in the wild state, and are usually known only as weeds of flax. Such are *Camelina linicola* Schim. et Spen., *Spergula maxima* Weihe and *Spergula linicola* Boreau (spurries), *Lolium remotum* Schrank, *Polygonum linicola* Sutulov, and others.

Polygonum linicola derives its origin from the widely distributed *P. lapathifolium*. *Camelina linicola* is derived from *C. glabrata* Fritsch, a cultivated (oil) plant, occurring, however, also in flax-fields (Zinger, 1909, p. 184). The ancestor of *Spergula maxima* is the common weed *Sp. vulgaris* Boenn. (Zinger, p. 261); in a similar manner *Sp. linicola* proceeds from *Sp. sativa* Boenn. *Lolium remotum* is a derivative of *L. temulentum* L. (darnel), a pest of spring crops, especially oats and barley.

All these "flax plants," although belonging to various families, growing in flax-fields, acquire the aspect of the true flax-plant. Flax cultivated for fibre is sown thickly to force the growth of the stalk, whereby fewer capsules are produced. The above-mentioned plants have a correspondingly thin, unbranched, elongated stem, and, as in flax, narrow, light-green leaves. The fruits of these weeds are similar in weight, as also partially in shape, to those of flax, being considerably heavier than the fruits of the corresponding

wild species (see Zinger, 1909, pp. 182-183, 282; Sutulov, 1915, p. 8).

All the progenitors of the "flax plant" species are very variable forms. They become weeds of flax because their germinal cells contain certain factors common to flax. When in a suitable environment, *Polygonum lapathifolium* revealed these factors, and became transformed into *P. linicola*, the same thing happening with *Camelina glabrata* and others. As is admitted by Zinger (p. 99), the modification of the vegetative organs of *C. glabrata*, involving the production of *C. linicola*, occurred without the intervention of selection; it was effected by external conditions alone; and only an increase in the weight of the seeds in *C. linicola* is due to selection. These seeds are so large that in size they approach those of flax, and in ordinary circumstances cannot be separated from them, while the smaller seed of the cultivated *C. glabrata* can be easily sorted from the seeds of flax. By means of selection *C. glabrata* may have been transformed into a noxious weed, the seeds of which have become so large that they can be separated from those of flax only with the greatest difficulty, and this circumstance has caused *C. linicola* to become a constant satellite of flax (Zinger, pp. 183-184).

But the possession of large seeds is a feature which had potentially existed earlier in the ancestors of all "flax plants." "Flax plants" in the absence of flax obviously consist of a series of elementary species, and this is attested by their great "variability," which is commented upon by all writers. When a plant potentially possessing large seeds occurs in a flax-field, an artificial (although unconscious) selection on the part of the flax-grower contributes towards the segregation of the completely developed forms.[1] In this case an elementary species (a pure line) with large seeds has

[1] We regard the selection of plants obstructing the flax crop as artificial, for in a state of nature such a phenomenon could have hardly taken place without the interference of man; and if it had, it would be a most exceptional case.

been segregated by artificial selection from a mixed population, and not single specimens with the largest seeds approximating the seeds of flax in size.[1]

A similar argument is applicable to the seasonal dimorphism of certain meadow grasses, discovered by Wettstein, which occur in two forms: one, a meadow form, fructifying before the time of hay-making; and another, growing on other lands than meadows, ripening after that period.

Vavilov (1922a, p. 85) has observed a striking case of mimicry, or convergence, in papilionaceous plants.[2] In Russia and Western Asia vetch (*Vicia sativa*) is often found as a weed in sowings of lentils (*Ervum lens*). There are varieties of vetches quite similar to ordinary lentils in the shape, colour and size of their seeds. "Most of these varieties flower and ripen simultaneously with lentils, and are perfect mimics of their 'models'—lentils." On the other hand, varieties of lentils were found which are quite similar in their seeds to ordinary round black-seeded vetches. "The rôle of natural selection in this case," says Vavilov, "is quite clear. Man unconsciously, year after year, by his sorting machines separated varieties of vetches similar to lentils in size and form of seeds, and ripening simultaneous with lentils. The same varieties certainly existed long before selection itself, and the appearance of their series,

[1] Besides the above-mentioned weeds, some others have been lately described. Zinger (1913) investigated *Alectorolophus apterus* Fries, which obstructs the crops of winter rye and is derived from *A. major* Reichenb (Scrophulariaceae). Upon reaching maturity the capsules in the latter burst open and shed seeds provided with wings. In *A. apertus* the capsules remain closed, and the seeds fall out when threshed with rye. The seeds of *A. apertus*, devoid of wings, remain with the grains of rye during winnowing. R. G. Betner (1917) has described a noxious spring race of *Lithospermum arvense* (*Boraginaceae*) obstructing spring crops, chiefly oats. Its period of vegetation, in distinction from the wild growing (winter) *L. arvense*, is confined to one season; it sprouts in spring simultaneously with the spring cereal crop, and towards the time of harvesting (middle of July) the latter terminates its cycle of development. The wild-growing *L. arvense* prolongs the period of flowering and fructification until August or September.

[2] Compare also Baroulina, 1920.

irrespective of any selection, was in accordance with the laws of variation."

A West Australian plant, *Loranthus quandang*, parasitic on the acacia, is so like its host in the size, colour and shape of the leaves, that in a state of nature it is difficult to distinguish them. Similar facts have recently been observed by Wettstein in Brazil, where the parasitic Loranthaceae imitate their hosts, the Lauraceae (Porsch, *pp.* 538-539).[1]

3. MIMICRY AND CONVERGENCE

If two butterflies are similar in colouring and mimic each other, it is obvious that they contain similar factors for coloration. Similar conditions cause these factors to be manifested in both species. From the point of view of the adherents of the theory of natural selection, similarity is the consequence of an accidental acquisition by one species of the characters of another. We assume, on the contrary, that the factors of similarity were present from the very beginning both in the imitator and in the imitated, and an impulse alone was needed for their manifestation.

This may be well seen from the following. Certain insects in their yellow and black colouring "mimic" wasps, Vespa, which can sting viciously. But a similar type of coloration first arose, not in Vespa, but in many Hymenoptera more lowly organised than the Vespidae, such as in the Tenthredinidae, Sirecidae, Cephidae, many Icheumonidae, Scoliidae, as also in the Apidae. Moreover, a black and yellow coloration occurs not only in Hymenoptera, but also in Diptera, Panorpidae, Lepidoptera, Neuroptera, Coleoptera, dragon-flies, and even in cockroaches. "Therefore," says Handlirsch (1906-1908, p. 1342), "insects in general are endowed with a predisposition to assume a 'wasp-like' coloration, and there is nothing astonishing in its being

[1] *Loranthaceae are really semi-parasitic. To this family belongs the mistletoe, Viscum album.*

exhibited by representatives of various orders." [1] Similarly a tendency towards a bumble-bee-like pubescence and coloration occurs in various groups of insects (Handlirsch, *l.c.* p. 1343).

The perspicacious Bates, author of the theory of mimicry, understood this. "It is perhaps true," he says (1862, p. 508), "that the causes which produce a close or mimetic analogy cannot operate on forms which have not already a general resemblance, owing to similarity of habits, external conditions, or accidental coincidence."

Punnett (1915, pp. 148-149) suggests that "the occurrence of mimetic resemblances is the expression of the fact that colour pattern is dependent upon definite hereditary factors, of which the total number is by no means very great. As many of the factors are common to various groups of butterflies, it is to be expected that certain of the colour patterns exhibited by one group should be paralleled by certain of those found in another group." This opinion is shared by Vavilov (1922a, p. 85) :—"Mimicry may be regarded as a general phenomenon of repetition of form, characteristic of the whole organized world; those usually impressive forms of mimicry which are found, for example, in butterflies, give an excellent illustration of the law of homologous variation."

In Chapter VI it has been shown that the geographical landscape lays a peculiar impress on its inhabitants, and produces the phenomena of convergence and parallelism. Mimicry undoubtedly belongs to the same class of phenomena, as is particularly well illustrated in the case of "flax plants" (see above, pp. 324-326).

It is sometimes very difficult to decide whether we have to do with mimicry or convergence. We may take a few examples.

[1] A wasp-like shape of the body and coloration may be observed, *e.g.* in Australian beetles of the genus Esthesis (Cerambycidae), in the Brazilian butterfly *Isanthrene profusa* (Syntomididae), in the South European butterfly *Memythrus tabaniformis* var. *rhingiaeformis* (Aegeriidae), and in the European fly *Sphecomyia vespiformis* (Syrphidae).

On the coasts of the Riu-kiu Islands, amongst coral reefs, occur two species of snake-like eels (Ophichthyidae). *Liuranus semicinctus* (Lay and Bennett) and *Chlevastes colubrinus* (Boddaert) ; their distribution in the west extends as far as the Malay Archipelago and even farther. In coloration they are remarkably alike,[1] recalling at the same time in shape of body and outward appearance poisonous sea-snakes, which are found in the same localities. Some observers have been inclined to interpret this as mimicry, but Werner found in the stomachs of poisonous sea-snakes some eels, *Chlevastes colubrinus*, which resembled the snakes in the shape of body, coloration and pattern.[2]

Two beetles from Mongolia, *Eupachys glyptopterus* and *Taphoxenus rugipennis*, both belonging to the family of Carabidae, but very widely separated from each other in the system, are both carnivorous, and are very much alike. The same applies to two caraboid beetles from Nova Zembla, *Amara alpina* and *Feronia imitatrix*.[3]

In Central America many species of brilliantly coloured harmless coral-snakes are known, which are said to imitate the poisonous Elaps, having the same coloration of black, red and yellow rings or bands. Elaps is, of course, regarded as being protected by its warning colours. But Gadow remarks (1911, p. 3) that both model and imitator lead a hidden mode of life, preying in the dusk and during the night chiefly upon other snakes. On the other hand, the enemies of Elaps are turkeys and peccaries ; neither against the former nor the latter are warning colours of any avail. Harmless snakes in elapoid dress are much more common in America than Elaps : thus in Mexico there are only two species of Elaps to no less than ten of " imitators." Besides, in the United States there are harmless " imitators " (genera

[1] Jordan and Snyder, 1901, pp. 866-867. For figure see D. Jordan, 1905, p. 233.

[2] Werner in Brehm's " Tierleben," vol. v.

[3] Semenov, 1900, pp. 623-624.

related to Coronella) in districts where no species of Elaps are met with, the range of the former extending far beyond that of the nearest species of the latter. Lastly, the variations of pattern in Elaps are manifold, and all these patterns and combinations of colour occur also in imitators, but rarely in the same district. The resemblances between *Elaps and some species of Coronella are very striking.* But the most common combination and patterns in *Elaps fulvius* are just the very kind that Coronella is unable to produce. Gadow's studies on coral-snakes have shown that both Elaps and its imitators display similar variations of colour and pattern. These variations "do not follow promiscuously, but upon predetermined lines, or rather in stages, the succession of which is fixed so clearly that they can be predicted. They are not cases of lawless variation, but represent orthogenetic variation" (p. 11).[1]

Cynipidae ("gall-flies," hymenopterous insects), as is well known, have enemies within the family, which lay eggs in the galls of strangers. It appears that the inquiline Cynipidae are very much like their hosts. Thus in the galls of the blackberry in North America occur the cynipid host Diastrophus and its inquiline Aulax. The latter shows the most striking resemblance in size, colouring and sculpture to Diastrophus. The one is the very counterpart of the other, showing hardly any differences except the strictly generic characters (Osten-Sacken, 1863, quoted from D. Sharp, 1899, p. 532).

4. PROTECTIVE COLORATION

Besides mimicry, a similar phenomenon, the colouring of animals to suit the environment, may be observed in nature. Thus, many polar animals are coloured white, the animals of the desert greyish-yellow, grasshoppers (Locusta) are

[1] The "mimetic analogy" between the venomous Elaps and harmless snakes of Central America was discussed by Cope as early as 1868 (cf. 1887, p. 105, pl. iii).

green, plaice adopt the hue of the sea-bottom, etc. All these are examples of *protective coloration*.

The origin of this is, of course, explained by the effects of selection on chance variations. But selection plays *no* part in this matter, as will clearly appear from the following illustrations.

The turbot (*Bothus*, or *Rhombus*, *maximus*), a flat-fish, is able, according to the observations of Pouchet, to vary its coloration in agreement with its surroundings: if it be placed in a vessel with dark walls, it becomes dark coloured; if with light, it becomes light coloured. But if the turbot be blinded, its power of adaptation to the environment is lost. The faculty of varying its colours increases with habit; five days are at first required for a light-coloured turbot to turn dark; the same specimen, put into a light-coloured vessel, in two days became light again, but on being again removed into a dark vessel, became dark in the course of two hours. A non-migratory cod occurs in the Norwegian fjords, which lives among thick growths of laminariae. It is distinguished by its reddish-brown colour, which recalls that of the sea-weeds. And yet the oceanic cod is grey. J. Petersen (1902) in a relatively short time succeeded in changing the colour of the cod in accordance with its surroundings. *Perccottus glehni*, an Amur fish of the family Eleotridae, allied to the Gobiidae, if placed in a white metal vessel will, in the course of 5-10 minutes, alter its black colour into a light yellow (Berg, 1912). Many cases of a similar kind could be recorded.

In addition to Pouchet's observations mentioned above, the following will show that in the flat-fishes (Pleuronectiformes) the protective coloration is not in the slightest degree due to the effects of natural selection. In all these flat-fishes, with eyes completely removed to one side of the body, the blind side is either perfectly white, or at least of a much lighter hue than the side provided with eyes. But, in those flat-fishes in which the eyes are not completely

transferred to one side of the body (such as, for instance, *Reinhardtius hippoglossoides*), either both surfaces of the body are coloured alike, or the blind one is a shade lighter than the other. It is a curious fact, that in species which normally have both eyes on one side of the body, there occur specimens in which the transposition of these organs to one side is not complete, and in such cases both sides of the body are coloured alike. Such cases have been described in the turbot (*Rhombus maximus*, *R. maeoticus*, *R. rhombus*), in the sole (Solea, see Gemmill, 1912), as also in *Pleuronectes pinnifasciatus* (P. Schmidt, 1916). The protective coloration of the flat-fishes is thus connected with the functions of the organs of vision, and is not controlled by selection.

The same conclusion may be arrived at from observations recently made on the newt (*Molge palmata* ; Oldham, 1915). Individuals living in a basin with a dark bottom are dark green ; when the bottom is yellow they turn yellow ; when it is white they become lighter coloured. The cause of this variation in colouring is due to contractions and expansions of dermal pigment cells. Blinded newts are incapable of adapting their coloration to that of the surroundings.

Przibram (1919) made a series of experiments showing that the coloration of animals may depend upon the chemical action of the coloration of the environment upon the "colouring" ferments of the organism. To such ferments may be referred *tyrosinase*, which is of much importance in the formation of dark pigments. This ferment, which was originally obtained from the mushroom *Agaricus melleus*, and subsequently from various animals, possesses the property of transforming (oxidizing) tyrosine and other chromogens into dark pigments or melanins in the presence of air. The intensity of the action of tyrosinase upon animal pigments varies under the influence of different physical and chemical agents. The adaptation of animals to the coloration of the environment is partly attributed by Przibram to the action of ferments sensitive to light upon the pigments

of the animal body. In the phenomena of adaptive coloration we thus encounter, to some extent at least, a certain kind of coloured photography, to which allusion was made in his time by the physicist Wiener (1895). It is obvious that all the above-mentioned processes take place in an orderly manner, never being due to chance.

We know, on the other hand, that many organisms possess definite types of colour variations: albinism is often met with in mammals and birds, brown and green variations occur among insects, etc. It is clear that natural selection must have contributed towards the distribution of these *pre-existing* variations in an appropriate environment: thus green-coloured animals ultimately occur amongst green-coloured plants, yellow in sands, white in snow-clad regions. We, therefore, cannot raise any objections to the following observations of Weismann (1909, p. 51):—"Many birds—starlings, blackbirds, swallows, etc.—occasionally produce white individuals, but the white variety does not persist, because it readily falls a victim to the carnivores. This is true of white fawns, foxes, deer, etc. *The whiteness, therefore, arises from internal causes, and only persists when it is useful.*" [1] In other words, the above-mentioned animals were in possession of the white colour factor (gene), its origin and manifestation standing in no relation to natural selection. The latter contributes only to a certain geographical distribution of the individuals which are in possession of a definite character.

Protective coloration in many other cases is effected, if not exactly in the same way, still in a similar manner.

5. PROTECTIVE RESEMBLANCE

By the term *protective resemblance* we cover those cases in which the animal or plant resembles surrounding objects in its whole outward aspect (and not only in colouring).

[1] The italics are mine.

Thus the South African plant *Mesembryanthemum calcareum* (of the family Aizoaceae, allied to the cactuses) possesses leaves extremely similar to the surface of pieces of the calcareous tufa among which it grows (Marloth).[1] A poisonous scorpaenoid fish, *Emmydrichthys vulcanus* Jordan, occurs on the shores of Tahiti in crevices of black lava, and both in shape and colour very much resembles lumps of lava (for

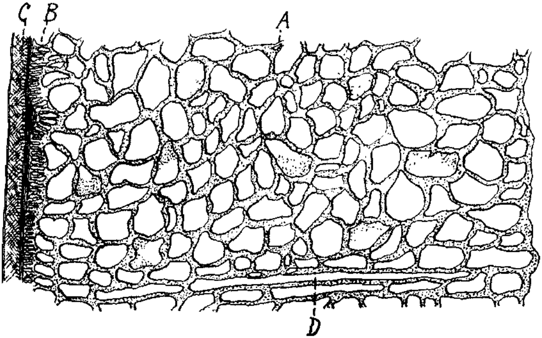

Fig. 32.—Portion of longitudinal section through the egg-shell of *Phyllium crurifolium*. (×100.)
A, external zone; *B*, median zone; *C*, internal zone; *D*, elongated alveoles. (From Henneguy, "Les Insectes." Paris, 1904, Masson).

fig., see Jordan, i, p. 180; ii, p. 436). Another scorpaenoid fish, *Synanceia verrucosa* L., from the Pacific shows resemblance to coral masses, in the clefts of which it lives (Jordan, i, p. 229, fig.). The Australian sea-horses, Phyllopteryx, in the form of their body and appendages very much recall the sea-weeds among which they live. The mollusc *Litorina obtusata*, attached to *Fucus vesiculosus*, closely resembles the vesicles of the alga (Piaget). Another

[1] To this resemblance attention was drawn for the first time by Burchell as long ago as in 1811 (see Poulton, 1909, p. 273). The same author observed in South Africa a plant ("Crassula") concealed by its likeness to the dung of birds (*ibidem*, p. 276).

mollusc, *Archidoris tuberculata*, living on the sponge *Halichondria panicea* in the North Sea, is very similar to the sponge in colour and form. The Malayan and Siamese spider, *Ornithoscatoides decipiens*, when sitting on a leaf, is wonderfully like freshly deposited birds' excrement. The same is true of many caterpillars. Thus the young caterpillars *Acronycta alni* and *Thyatira batis*, from the Government of Petrograd, very much resemble birds' excrements.[1]

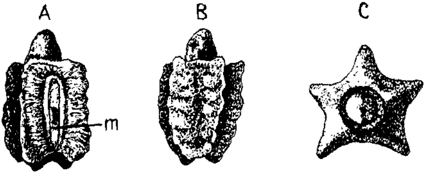

Fig. 33.—Egg of *Phyllium crurifolium*, resembling the fruit of Umbelliferae. *A*, from the side where the micropyle (*m*) is situated; *B*, from the opposite side; *C*, from above.
(From L. F. Henneguy, "Les Insectes." Paris, 1904 Masson.)

Eggs of stick- and leaf-insects (Phasmodea) are remarkably like seeds, the similarity not being confined to their outward appearance: the microscopical structure of the wall of the egg-shell (chorion) in *Phyllium crurifolium* recalls vegetable tissue (Henneguy, 1904, pp. 294-5). (Fig. 32.) Externally the egg strikingly resembles the fruit of Umbelliferae. (Fig. 33.) The eggs, like seeds, are scattered by the insect on to the ground, where they sometimes remain lying for two years. The case of the butterfly Kallima[2] and the leaf-insect Phyllima is universally known.

This phenomenon is undoubtedly much more complex than mimicry and protective coloration. We must frankly admit that hitherto we have no rational explanation of the

[1] Portschinsky, "Horae Soc. Entomol. Rossicae," xix, pp. 80-81, 70 71, table x, fig. 8, 6c.

[2] Among Russian butterflies *Libythea celtis*, occurring in the south of this country, is similar to the leaf of Celtis, on which its caterpillars feed (Kuznetzov in Sharp (Russ. ed.), 1910, p. 849).

cases of protective resemblance, nor of much else besides. And it is far better thus openly to confess our limitations, than to lull ourselves to self-complacency by pseudo-arguments, such as that similarity between a caterpillar or a spider and birds' excrements may ultimately be due to the effect of accidental variations, etc. Any other explanation, from the point of view of probability, would be much more admissible, although it must be owned that all the interpretations hitherto offered have failed to account for the phenomena in their totality. Thus Eimer (1897) says that the development of the colouring and venation of the wings in various butterflies of the group Kallima tends in general to follow the direction of similarity to the leaf, and that forms could be selected so as to present an ever-increasing series of similarity. And so, on this theory, the resemblance of Kallima to the leaf would be the result of chance; but such a kind of chance would in any case be much more likely of occurrence than that heaping of chance upon chance to which selectionists are compelled to resort.[1]

Similarity is in certain cases undoubtedly due to the animal instinctively choosing a habitation suitable to the colouring and shape of its body. But such an explanation may be held to be applicable in but a very few cases.

6. "WARNING" COLORATION

That the explanation of so-called "warning" colours by means of natural selection is inadequate has been excellently demonstrated by Danilewsky (pt. ii, pp. 165-166). It is impossible to conceive, he says, that birds are so foolish as not to become convinced before long that caterpillars with all their awe-inspiring attitudes and terrifying ocelli are, after all, very good eating. Birds manage to subdue their awe when they perch on scarecrows, and to learn also to fear man. "And, if it is so, all the many thousand

[1] See, for example, Plate, "Selektionsprinzip," p. 208.

years' labour of selection with caterpillars would not only be in vain, but would not even be able to arise at all, for as soon as these intimidating peculiarities began to form, the birds would have ample time to get used to them, and no advantage would thus be gained. That birds should become accustomed to the forms of caterpillars is much easier to suppose possible than, for instance, a parallel course of variation in clover and bumble-bee-like insects; the end in the first case would be achieved by means of the intellectual faculties of birds, which can be adapted to circumstances, while in the second it would be gained through a parallel development, and this, owing to variability being so indefinite, is quite improbable."

These perfectly just arguments are radically subversive of those of Weismann. They may even be amplified in a considerable measure to apply to the entire theory of mimicry and protective adaptation, as elaborated by Darwin, Wallace and Weismann. Every resemblance, according to the theory of these naturalists, must develop gradually; but just as gradually would be sharpened and perfected the sense organs, say, of birds, by the same hypothetical selection: all the artifices of the deceiving animals would thus end in nothing. It is the same with the practice of marine warfare: the more the thickness of armour in battleships is increased, the more effective is rendered the penetrating power of projectiles.

The object of the foregoing examples has been to show that the phenomena of resemblance, or convergence, among organisms, due to a similarity in the conditions of existence, are extremely numerous and manifold. Mimicry is but one particular case of convergence, to which there are no grounds for attributing an exceptional origin or importance. By mimicry, as we have seen, is understood a similarity between two organisms which is useful to one of them. If no utility can be demonstrated, it is regarded as a case of convergence.

CHAPTER IX

POLYPHYLETIC ORIGIN OF SIMILAR FORMS

1. POLYPHYLETIC ORIGIN IN COMPARATIVE ANATOMY AND TAXONOMY

By the comparison of Dipnoi and Amphibia, Pterosauria and birds, Saurischia and Ornithischia, Bennettitales and Anthophyta, and many others, considered in Chapter IV, we have shown that the groups which, being derived one from the other were thought to have been descended from one ancestor (monophyletic), really owe their origin to several, or are polyphyletic. Thus it was formerly assumed that all dinosaurs represent a single group, and that Ornithischia were derived from Saurischia; but it has now been shown that it is impossible to derive Ornithischia from Saurischia, and that the two groups are really two parallel branches. Therefore their similarity is not due to consanguinity, but to an evolution according to a definite law, *i.e.* based upon nomogenesis, not chance.

The class of Cephalopoda is polyphyletic: Ammonitidae and Nautilidae have developed independently (Hyatt). The phylum of Arthropoda owes its origin to different roots; the Crustacea and Arachnida, as is supposed, to secondary-coelomate mesomeric (with a moderate number of segments) worms; the Tracheata, *i.e.* myriapods and insects, to secondary-coelomate polymeric (with numerous segments) worms. According to Walcott ("Cambrian Brachiopoda," U.S. Geological Survey, Monogr., li, 1912) the Cambrian Brachiopoda appear as three distinct groups—Protremata,

Atremata, Neotremata. It is impossible to derive these groups *from any real common ancestor.* There are no intermediate links between horn-shelled and lime-shelled brachiopods, nor between single genera. As a matter of fact, we observe a parallel development of diverse genera.[1] The various classes and orders of Fungi may have originated from different groups, *i.e.* amoeboid organisms, colourless Flagellata, homoflagellate green Algae. and red Algae (N. Busch).

It was formerly assumed that seed-plants arose from the Pteridophyta, the seed-ferns (Pteridosperma or Cycadofilices) being regarded as a connecting link between the two. But it has now become evident that the majority of the carboniferous " ferns " were not ferns, but pteridosperms, *i.e.* true gymnosperms. This circumstance compelled the palaeontologists to revise their views on the origin of the seed-plants. Ferns are unknown before the Upper Devonian. On the other hand, in the Middle Devonian occur true gymnosperms, such, for instance, as Palaeopitys. The Upper Devonian Callixylon was more highly organised than the pteridosperms. " If we may judge by anatomical characters," says D. Scott (1923, p. 59), referring to the above-mentioned facts. " the seed-plants seem to have been in advance of the spore-plants from about the time of the earliest known land flora." Pteridophyta and gymnosperms are two parallel independent phyla. We have no reason to believe that pteridosperms are descended from ferns, the fern-like features of their foliage being in most part due, according to Scott, to parallel development.

If we now turn to the origin of angiosperms, we may quote the opinion held by Velenovsky (1905, p. 31), that gymnosperms and angiosperms are parallel branches, which have developed since time immemorial side by side, from different, independent ancestors. As we have seen (Chap. IV), the *origin of angiosperms, according to* Kuznetzov

[1] See Wilkens, 1919.

(1914, 1922) is diphyletic, the Polycarpicae arising from Bennettitales, and the Monochlamydeae from the supposed "Protogymnospermae." Karsten (1918) shares the same view as to the polyphyletic origin of angiosperms. "Is it not probable," he asks, "that angiospermy should have arisen several times from gymnospermy, just as heterospory has many times arisen from homospory in ferns?" However, unlike Kuznetzov, he believes that the ancestors of angiosperms were two different groups of Gnetales: from Ephedra-like gymnosperms are descended the Monochlamydeae, and from Gnetum-like the Polycarpicae. Gothan (in Potonié, 1921, p. 488) believes likewise that Polycarpicae and Monochlamydeae are two separate phyla, having an independent origin. As a proof of the polyphyletic origin of angiosperms, he adduces the circumstance that angiosperms arise simultaneously at different points of the globe, being at once differentiated into separate groups. According to the same author (1921, p. 483), the Pteridophyta consist of four entirely independent series, namely, Psilophytales (Rhynia and Hornea),[1] Lycopodiales, Articulatae (=Equisetales) and Filicales.

As the knowledge of the structure of plants and animals grows more exact, and the field of palaeontology becomes widened, the number of cases of polyphyletic origin increases. And yet the principle of polyphyletic origin undermines the very foundations of "selectionism." Therefore the comparative anatomists of the dominant school are usually adherents of monophyletic origin, attributing the origin of every phylum, class and order to a single ancestor: as chance is called upon to respond to many demands, it is preferable, as Spemann (1915, p. 80) justly observes, to trouble it as seldom as possible.

Haeckel was a monophyleticist. He derived all vertebrates (including Amphioxus, of course) from a single

[1] The recent Psilotaceae, as possessing sporophylls, are referred by Gothan to the Lycopodiales.

ancestor, the problematic "Prochordonia" (1895, p. 4), which gave origin both to vertebrates and tunicates, and was derived, in its turn, from Enteropneusta (pp. 13, 15). And yet such a conception is clearly inadmissible, for we have shown above (pp. 99 and 169) that the notochord, the gill-slits, the dorsal nervous system, have undoubtedly each and all been independently formed in various groups of animals: in Balanoglossus, Tunicata, Amphioxus, Cyclostomata, and in the ancestors of true fishes. Therefore not only the Chordata, but also the vertebrates themselves, are polyphyletic groups: they have evolved not from one root, but in parallel lines, some of which have developed more rapidly, and others more slowly.

The well-known palaeontologist Abel thinks that the very idea of a "polyphyletic origin" of any taxonomic group, being absurd, must be cast aside. If it appears that a group, which was formerly held to be monophyletic, includes forms possessing a complex phylogeny, it should be subdivided into as many systematic units as there were phylogenetic lines entering into its composition (1919, p. 5).

To create a new name is not a very difficult matter. But a fact remains a fact. *Similar* forms have been produced from various stems, and that is what we mean when we speak of polyphyletic origin. Every new class, sub-class, order, etc., established on the assumption of it being derived from a separate root, is yet another proof of the inadequacy of selectionist views and a confirmation of the truth of nomogenesis.

If we turn to the history of the classification of plants and animals, we shall see that the number of phyla, classes, orders, etc., continually increases, and this increase is, in an overwhelming majority of cases, due to authors realising that they are unable to derive one group from another, *i.e.* it testifies in favour of polyphyletism.

Let us take an example. In the time of Darwin fishes were classified according to the system of the celebrated

J. Müller (1844), who recognised six sub-classes in the class—(1) Leptocardii, *Amphioxus*, (2) Marsipobranchii, lampreys, (3) Elasmobranchii, sharks, (4) Ganoidei, (5) Teleostei, bony fishes, with six orders, and (6) Dipnoi. Soon after, the Leptocardii were separated as a distinct sub-phylum, Acrania, and the lampreys were placed in a super-class, Agnatha (jawless), containing the class Marsipobranchii; the Teleostei were subdivided into many orders (Cope, 1870-71). Subsequently Gill, Jordan and Tate Regan promoted the Elasmobranchii to the rank of a class, and distinguished about thirty orders of Teleostei. Finally, the following division of the lower vertebrates (Craniata), aquatic and provided with fin-like extremities (if present), was submitted by me (1922):—

A. ICHTHYOMORPHI. Fish-like animals. Without paired extremities; jaws are either wanting, or, if present, are without teeth.
  Series I. *Marsipobranchii* (or *Cyclostomi*). Lamprey-like animals.
    Class 1. Myxini. Hag-fishes.
    Class 2. Petromyzontes. Lampreys.
  Series II. *Placodermi*. Hard skeletal structures are present.
    Class 3. Ostracodermi. Sub-classes: Anaspida, Pteraspida, Cephalaspida.—Silurian, Devonian.
    Class 4. Pterichthyes.—Devonian.

B. PISCES. *True Fishes*. Paired extremities, if not reduced, are always present. Jaws always present, with teeth.
  Series III. *Coccostei*.
    Class 5. Coccostei.—Devonian, Carboniferous.
  Series IV. *Chondrichthyes*. Cartilaginous fishes (without true bone).
    Class 6. Selachii. Shark-like fishes.
    Class 7. Holocephala. Chimaeras.
    Class 8. Acanthodii.—Devonian—Permian.
  Series V. *Osteichthyes*. Bone in skull and vertebral column. Jaws covered with bones, at least partially.

Class 9. Teleostomi. Higher fishes. Sub-classes: Crossopterygii (of which the recent examples are Polypterus and Calamichthys) and Actinopterygii. The latter are subdivided into two groups: Chondrostei with one order, and Teleostei with thirty orders.

Class 10. Dipnoi.

The Marsipobranchii are neither the descendants of the Acrania (Amphioxus), nor are they the ancestors of true fishes. Placodermi and Coccostei are singular Palaeozoic fish-like animals and fishes, from which it is not possible to derive the other classes. Cartilaginous fishes represent a separate branch, parallel to the series Osteichthyes. This latter series cannot be derived from the Selachii: in Chondrichthyes the solidification of the vertebral column is accomplished by the impregnation of the cartilage by lime, whereas in the Osteichthyes the cartilage is replaced by bone. The Acanthodii form a much specialised lateral branch (see p. 101). It is possible that the Dipnoi owe their origin to the same stem as the Teleostomi, but constitute a terminal branch of development, so highly specialised in the direction of terrestrial vertebrates (see p. 171) that they should be separated into a distinct class. Thus, Müller's class Pisces had to be broken up into ten, and this is mainly due to the old class Pisces being of a polyphyletic origin.

But the foregoing system, even if we allow for the imperfection of the palaeontological record, is probably also artificial, for our classes are undoubtedly polyphyletic units. Can it be supposed that Teleostomi or Selachii, for instance, are monophyletic, *i.e.* that each one is derived from a single progenitor or a single group?

A strict adherence to the monophyletic principle is generally bound to lead to absurdity. For in that case we should have to admit that all mammals (or even all vertebrates) or all angiosperms are derived from one individual. For, if they owe their origin to many individuals, their

development would be governed by analogy and convergence, not by homology. But it is quite inconceivable that all vertebrates, for instance, should be derived from a single pair.

Polyphyletic origin was to a certain extent admitted by Darwin. He believed "that animals are descended from at most only four or five progenitors, and plants from an equal or lesser number" ("Origin of Species," chap. xv, p. 424). "At least all the members of the same class have descended from one progenitor," but it is more probable "that all living creatures have descended from a single prototype."[1] At the present time, however, such an opinion would find no support from the most extreme adherents of the theory of natural selection. Not only do phyla, classes and orders not infrequently prove to be polyphyletic, but such is often the case with lesser taxonomic divisions. Darwin's law of convergence is thereby undermined.

Systematists are often induced to subdivide a genus containing many species into several genera. Thus, fishes of the genus Cottus (Cottidae, miller's thumbs), as it is defined in the Catalogue of the British Museum (1860), are now split up into many genera, Cottus, Myoxocephalus, Ceratocottus, Gymnacanthus, etc. Mountain finches of the genus *Montifringilla*, as defined by the British Museum Catalogue (1888), have been separated into five genera (Bianchi, 1907, 1908), etc. It is generally presumed that the characters in which these new genera resemble each other are an inheritance from their common ancestor, while the features in which they differ (differential features) are a new acquisition. In other words, it is assumed that resemblance is something old, and difference something new. This follows also from Darwin's law of the divergence of characters.

Palaeontology, however, very often offers no support to this conception. As we had occasion to see in Chapter III,

[1] "Variation of Animals and Plants," i, p. 13; see also concluding chapter, xxviii, p. 430.

§ 3, genera understood *sensu lato* are not infrequently *polyphyletic*, *i.e.* owe their origin not to one ancestor, but to several. (These heterogeneous genera are the very ones that have to be subdivided.) But this means no more than that in the given case the differences between the smaller genera is a primary phenomenon, whereas similarities, which on the whole predominate in the outward appearance, have been to a considerable degree elaborated independently in the process of evolution, or are the result of convergence.

Let us consider some cases of polyphyletic genera which have been proved to be so by palaeontology.

The forms of the bivalve Mollusca which are united in the genus Dreissena, as has been palaeontologically verified by Andrussow (1897, p. 613), develop independently from at least two branches of the genus Congeria. The author mentioned alludes to the observation of Oppenheim (1891) that smooth-shelled Hydrobia have in Semigradia, Greece, and, apparently, in Italy, independently given rise to the keeled Pyrgula. The brachiopods Strophalosia have developed polyphyletically from the Carboniferous Productus (Yakovlev, 1920, p. 264).

Amongst ammonites the genera Phylloceras, Lytoceras, Arietites, Perisphinctes, Hoplites and many others exhibit marks of polyphyletic origin, or, to put it differently, *separate groups of species, composing every one of these* genera, display a parallel development. Among Gastropoda the following are proved to be polyphyletic: Pleurotomaria, Trochus, Paludina, Turritella, Nerinea, Cerithium, Nassa, Pleurotoma, Murex and Conus; among the bivalves—Ostrea, Pecten, Trigonia, Pholadomya and Hippurites; among the Cephalopoda—Orthoceras and Nautilus; among the Brachiopoda—Strophalosia, Productella, Spirifer, Rhynchonella and Terebratula; among mammals—Mastodon, Elephas and many others.[1]

The following case, relating to several wingless rails

[1] Depéret, pp. 127, 144; compare also Yakovlev, 1920.

(Rallidae), is extremely interesting (Gadow, 1893, p. 101). The Mauritius was inhabited by a flightless rail, *Aphanopteryx bonasia*, now exterminated. A similar bird from Rodriguez, exterminated as late as the eighteenth century, is called *Erythromachus leguati.* Half-fossilised bones of a closely related genus, Diaphorapteryx, have been discovered on Chatham Island, east of New Zealand. The bones of all these genera have been examined by Gadow. Had they all been discovered in one island, he says, they would be regarded by everyone as species of one genus. The common source from which all the three above-mentioned "genera" must have been produced were rails of a type which can be imagined to have consisted of the combined characters of the recent genera Porphyrio + Tribonyx + Ocydromus. Our genera have probably descended from such a rail of the Mesozoic era, when the distribution of continents was not the same as now. Aphanopteryx, Erythromachus and Diaphorapteryx, says Gadow, morphologically constitute but one genus, for the same final forms have been produced from one common fundamental stock. But genetically we have to do with three analogous "isomorphic" or convergent genera.

The African ostriches (Struthio) and the American rheas have a similar outward appearance and many common points of structure. But there are also such radical differences between them that Fürbringer (1888, p. 1565) decided to separate them into two distinct orders. "Between Struthio and Rhea," he says, "genealogical differences, which go very far back, are present; *the dissimilarities between the two birds were once much more striking and externally apparent.* But similar conditions of life among which both species dwelt throughout the course of ages, gradually veiled the radical distinctions and produced a considerable resemblance between them in their outward aspect" (p. 1442).

The principle of polyphyletic origin thus leads us to the

following conclusion, which may at first sight seem paradoxical: points of resemblance in two forms may represent something secondary, acquired and new, whereas points of dissimilarity are something primary, inherited and ancient. This law is the antithesis of Darwin's law of *divergence*. I do not want to deny the latter. But alongside that law, and dominating it, operates the law of *convergence*.[1]

If, as has been shown in Chapters III and IV by numerous examples, convergence affects the most essential organs and leads to a resemblance between groups very far removed from each other, can there be anything surprising in the fact that forms which we conventionally refer or have referred to one genus, should have been produced by means of convergence (*i.e.* development in a determined direction) from two distinct genera ?

It is truly remarkable that palaeontology in no way displays transitional forms between phyla and classes, and, possibly, not even between orders. Thus, we are ignorant of transitional forms not only between vertebrates and invertebrates, fishes and tetrapods, but even between cartilaginous (Chondrichthyes, such as sharks, etc.) and higher fishes (Osteichthyes); in spite of a wonderful affinity between reptiles and birds, no transitional forms between them are known hitherto. Formerly, this circumstance was accounted for by the imperfection of the geological record; but it is none the less surprising that the deeper our knowledge penetrates into the domain of fossils, the further back recede genetic interrelations, which, as it were, ever elude our grasp. True, we know a number of groups that exhibit in their structure an intermingling, as it were, of peculiarities of two different orders or classes: such groups are generally alleged to be transitional. Thus, the Dipnoi have been regarded as a transitional stage on the way from fishes to amphibians, Acanthodii as a step from Selachii to higher

[1] The subject has already been discussed in the beginning of chap. iv p. 156).

fishes, Bennettitales as a connecting link between gymnosperms and dicotyledons, etc. But a more careful examination reveals that in all these cases terminal branches of evolution are represented, and not the transitional links so eagerly sought for. It is remarkable that all such "transitional" forms combine characters of high development with those of a very low one: the progressive features have been acquired, as was shown above (Chap. III) through phylogenetic acceleration. It may be held as a rule that all forms which have advanced too far in evolution, and in which progressive and primitive characters are combined, are *doomed to extinction.* Just as natural selection tends to preserve the standard within the confines of a species, so also does it operate within the limits of higher taxonomic groups, such as classes. It cuts off groups that have lagged too far behind, and also those which have advanced too rapidly, and so preserves, as it were, the golden mean.

We must repeat that a combination of characters of various styles is no proof of "transition": organisms, as may be inferred from modern genetics, generally consist of factors, which develop in a great degree independently of one another. Both palaeontology and comparative anatomy confirm this in the most striking manner.

"The developing animal world in its entirety," says Depéret, "may be imagined, as it were, in the shape of an assemblage of an infinite multitude of phylogenetic branches which evolve throughout longer or shorter series of geological epochs, parallel to each other and nowhere uniting. Every one of these branches, with varying speed, reaches a condition when mutations on a large scale are produced with very much specialized characters, and then vanishes, leaving no descendants. Whenever a branch disappears through extinction, it is supplanted, so to say, by another, which, having hitherto developed more slowly, will pass through the phases of maturity and decadence, in its turn also to perish."

Very valuable suggestions on polyphyletic origin and convergence have been put forward by Beketov (1896, pp. 9-10). There is no foundation for presuming, he says, that organic life originated in only one single spot on the earth. Moreover, since it is very unlikely that the conditions of life were from the beginning everywhere the same, the arising primary organisms could not have been identical in their structure.

On the other hand, the genetic interrelationship of organisms is, in Beketov's opinion, very much exaggerated. "There are very few, or no true, transitional forms between groups of organic beings. Even between genera and species they are far from being as frequent as many assert." To account for the absence of transitional forms, Darwin resorts to the suggestion that they were insufficiently adapted, and had therefore perished in the struggle for life. And yet, according to Beketov, "in whatever manner organic matter arose, it must in any case have been produced from pre-existing elements, under existing external conditions, and subject to a predetermined purpose which is life itself. In a word, the problem was to build under existing conditions from material which was to hand. Can it therefore be wondered at that all organisms in their chief and essential characters are similar to each other" (p. 9). For the sake of comparison Beketov points out that rock-salt *crystallises into cubes in America, as well as in Europe, but* it could hardly be claimed by anybody that all salt crystals have been derived from a single one, and that they are connected by blood relationship. On these grounds Beketov maintains that the number of primary progenitors was very considerable.

The distinguished palaeobotanist, Zeiller, held similar views (1900). Most of the principal groups of the vegetable kingdom, he says (p. 373), were as sharply defined from the very beginning of the known geological record as they are now.

The foregoing considerations prevent us from sharing the opinion of Darwin, who explained the absence of transitional varieties by these having existed in lesser numbers than the forms which they connect, and, as a general rule, being exterminated in the struggle for existence ("Origin of Species," chap. vi, p. 134); and, besides, "there will be a constant tendency in the improved descendants of any one species to supplant and exterminate in each stage of descent their predecessors and their original progenitors" (*ibidem*, ch. iv). Similarly, Bianchi (1907, p. 373) thinks that all taxonomic divisions, from sub-species and species to classes and phyla, have been produced by means of *the extinction* of a greater or lesser number of connecting links. In my opinion, the boundaries between taxonomic units are only in very few cases due to extinction: such may have been the case, though very rarely, with small units as "natio," sub-species, species, genus. There are only two causes capable of accounting for a break between two neighbouring groups. They are :—

1. *Polyphyletic origin*, *i.e.* derivation from two distinct sources; it is obvious that in this case there could be no connecting links from the beginning.

2. *Transformation of a considerable number of individuals into a new form*; in the operation of this cause, affecting small taxonomic divisions, such as "natio," sub-species and species, extinction, as a general rule, cannot be of any special importance in constituting a break between two neighbouring forms.

Admitting, on the other hand, the polyphyletic origin of separate groups of the vegetable and animal kingdoms —not only extensive groups such as phyla, but smaller ones,—we fully share Bianchi's (1907, p. 375) view on the necessity of splitting up a genus until it be cleared of all heterogeneous species.

2. POLYTOPICAL ORIGIN OF THE LOWER TAXONOMIC UNITS

We are able to record a sufficient number of well-established cases of the origin within the limits of one species of identical forms in various places, *i.e.* morphas, aberrations, "nationes," sub-species. These cases are described as *polytopical*, or independent formations: they represent a particular case of polyphyletic origin.

The Salmonidae, belonging to the genus Salmo and to allied genera (such as Salvelinus, Oncorhynchus), are generally anadromous fishes ascending streams from the sea for spawning. But in certain cases the sea fishes remain permanently in the fresh water, where they give rise to dwarf forms, extremely like the brook trout. In such a case, these brook-trout varieties are polytopically produced. Here we have an interesting double case of convergence in so far as it affects various species, and of polyphyletic origin. These varieties are hereditary, so long at least as the conditions remain invariable. They have been described in (1) the sea trout, *Salmo trutta*, and its sub-species, in Europe, the Caucasus and Turkestan. In the lakes of Europe and the Caucasus a form is produced under the name of morpha *lacustris* (lake trout), and in the brooks of Europe, the Caucasus and Turkestan the morpha *fario* (brook-trout),[1] (2) the masu, *Oncorhynchus masu*, in Japan and the coast province of Siberia, (3) the red salmon, *Oncorhynchus nerka*, in Japan and North America (this form has been described as *Salmo kennerlyi*), and (4) the char, *Salvelinus alpinus malma*, in the coast province of Siberia, Sakhalin, Kuril Islands, and North Japan (this form, described as *Salmo pulvius*, is called " forel " (brook-trout) in Nikolaevsk on the Amur).

The possibility that these fresh-water forms had arisen in one spot and had then spread over their present area must be rejected at once. On the contrary, the sea form, *e.g.* of

[1] Berg, 1916, pp. 46-48.

the char, gave origin to identical fresh-water varieties on the continent of Asia and in Japan.

Analogous cases occur in the kingdom of plants. In various parts of the Alps the sorrel *Rumex acetosella* has given rise to a dwarf variety, *minima* Wallr.

I shall give another illustration of the production of identical forms in various places. Recently (1916) I have described parallel forms produced in the lakes of Northern Russia and of Sweden, and also of North America, by the marine four-horned bull-head, *Myoxocephalus quadricornis*, a fish of the family Cottidae, a distant relative of the common fresh-water miller's thumb (*Cottus gobio*).

The marine *Myoxocephalus quadricornis* inhabits the Baltic Sea, the Arctic Ocean and the Behring Sea. It reaches a length of 325 mm., and is distinguished by the presence of four prominent bony protuberances behind the eyes, whence its name " four-horned." Both in Lakes Mälar (on which Stockholm is situated) and Ladoga (in Russia) occurs the same morpha *lönnbergi*, distinguished by a lesser development of its " horns " and by its smaller size. Lastly, in Lake Onega, as also in the Swedish lakes Wetter, Wener and Fryken and in the Great Lakes of North America, a morpha *relictus* has been found, in which the horns are usually absent or very slightly developed, the length of the body falling to 100 mm. It is obvious that the morpha *lönnbergi* has independently arisen in Russia and Sweden, and the morpha *relictus* independently in North America, Sweden and Russia.

Cases in which two nearly identical forms have arisen from a homogeneous stock parallel to one another in two disconnected regions have been called by Semenov-Tian-Shansky (1910, p. 29) " isokinetic."

Isokinetic transformations, similar to the above-mentioned one of the bull-heads, have been experienced by certain Crustacea. In the Baltic Sea occurs *Mysis oculata* ; it is represented in lakes Ladoga and Onega, in several lakes of Finland, North Germany, Denmark and Ireland and in the Great Lakes of North America by the form *relicta*, which is distinguished by its small size and a weaker armature of the

telson and caudal appendages (Ekman, 1913). The adult *Mysis relicta* recalls the young *Mysis oculata*. It is very remarkable that *Myoxocephalus quadricornis* morpha *relictus* likewise differs from its marine congeners in its smaller size and in its weaker armature. The adult individuals of the lake *Myoxocephalus relictus* are very like the young forms of the marine four-horned bull-heads. The parallelism with the Mysidae is complete. The marine crustacean *Limnocalanus grimaldii*, which gives rise to the form *macrurus* in the fresh-water lakes of Central Europe and North America (see Ekman), is analogous to the above-mentioned Mysis.

In all the foregoing cases we thus see an independent origin of the same forms in different places.

The European snail, *Helix arbustorum* (or, in the modern nomenclature, *Helicigona arbustorum*), falls into a number of local forms, very much resembling each other, but apparently having arisen independently (Pilsbry, p. 306).

The dogs of the ancient Peruvians belonged to different breeds, which *exhibit a remarkable likeness to the dogs of Europe*. Amongst the mummies of Peruvian dogs may be distinguished (1) collies, which in the Old World are derived, as is supposed, from the Indian wolf *Canis pallipes*, (2) turnspits or dachshunds, with very crooked fore-limbs, (3) bulldogs, which in the Old World are supposed to have descended from the Tibetan wolf *Canis niger* (Bogdanov, 1913, pp. 124-5, 127).

Among botanists, Briquet (1901), who has studied the flora of Corsica, supports the view of a polytopical origin of species. In his opinion *Cerastium thomasi* owes its origin to *C. arvensis* independently in Corsica and the Abruzzis, as does *Myosotis pyrenaica* in the Pyrenees and in Corsica to *M. silvatica*, and *Silene alpina* in the Alps and Sicily to *S. inflata*, etc.[1] Other authors disagree with Briquet on that point, maintaining that the Corsican habitat is due to

[1] See on the subject Lotsy, "Deszendenztheorie," ii, 1908, p. 486 *seq.*

the transportation or immigration of the plant. Engler, however, although denying the polytopical origin of species and genera, is disposed to recognise it in the case of varieties. But he admits that *Viola parvula* has descended from *V. palustris* independently in Corsica, Sicily, Greece and Crete (and, as Lotsy observes, ii, p. 488, also in the Canary Islands, North Africa, Spain and Eastern Asia).

Ettingshausen (1894, pp. 309 *seq.*) likewise maintains that identical species of plants may have been derived in different localities from identical stock; such a kind of "polygeny" he considers to be inadmissible in reference to widely spread species, which, moreover, trace their origin to Tertiary and even to Cretaceous forms.[1]

In Russia, as in Western Europe, the spurry, *Spergula arvensis* L. (more correctly *Sp. vulgaris* Boenn.), a common weed, is transformed in flax-fields into *Sp. maxima* Weihe, which is distinguished by its taller growth, its larger seeds and incapacity to open widely its capsules in order to shed the ripened seeds (Zinger, 1909, p. 261). Another closely allied species of the pernicious spurry, *Sp. sativa* Boenn., in flax-fields gives origin to *Sp. linicola* Boreau, a form with large naked seeds, copying those of flax. The spurry *Sp. linicola*, was originally discovered in France among flax in the valley of the Loire, and was subsequently found in Russia by N. Zinger. There can be no doubt that the "flax" spurries, both *Sp. maxima* and *Sp. linicola*, arose from parental forms independently in Russia and in Western Europe. (The wild *Sp. sativa* has apparently descended from the wild *Sp. vulgaris.* They are both cultivated. Each of these *wild* species has produced in flax-fields a *noxious* species; *Sp. vulgaris* has produced *Sp. maxima*, and *Sp. sativa, Sp. linicola.* (See Zinger, 1909, p. 280.)

Let us now take the case of a recent polytopical origin of genera.

[1] *However, the hypothesis of Ettingshausen is quite inapplicable to* certain examples set forth by himself, such as the bipolar distribution of the genus Carex. For the interpretation of the bipolar phenomena I have supplied another explanation (Berg, 1923).

In the opinion of Michaelsen (1905), a well-known authority on the oligochaete worms, species of the genus "Microscolex" at different times and in different localities have diverged from various species of the genus Notiodrilus. In one of the islands of the Crozet group Michaelsen discovered two species of related worms, one with genital organs of the *Notiodrilus* type, another with *genitalia* as in Microscolex; yet both species were similar as regards their peculiar coloration, distribution of the chetae, glandular modification of the integument in the region of the genital pores, the shape of the prostates (spermiducal glands of Beddard), etc. Hence *Michaelsen inferred that Microscolex* had arisen from Notiodrilus on the spot. Consequently, in other places other species of Microscolex have descended from another species of Notiodrilus. Microscolex has thus originated at least twice, from distinct progenitors and in different places, *i.e.* polyphyletically. Stephenson (1921) mentions some similar cases in Oligochaeta of the same family Megascolecidae. In the Eastern Himalayas occurs an oligochaete worm *Perionyx annulatus*. From the presence of micronephridia this species ought to be referred to Megascolex, but *P. annulatus* possesses at the same time a complex of characters typical of Perionyx, and occurs, moreover, in the centre of distribution of this latter genus. Stephenson presumes that in the Himalayas there has diverged from Perionyx its own representative of the genus Megascolex, which thus appears to be of diphyletic origin. But in addition, there are grounds for assuming that in Ceylon several species of Megascolex have been derived from Notoscolex. Similar relations between Megascolex and Notoscolex exist in New Zealand also. Thus species anatomically belonging to one and the same genus, Megascolex, arose from two distinct, less specialised genera, and such a process occurred at least three times. Michaelsen gets out of the difficulty by uniting the two genera Notoscolex and Microscolex into one, as he had already united Microscolex

and Notiodrilus. But similar cases among Oligochaeta are frequent, and the fusion of similar "illegal" genera into one would not solve the question. The course of evolution in Oligochaeta of the sub-family Megascolecini is, in general, predetermined ; it may affect certain modifications in the nephridia, as in the line of Megascolides, or in the chetae, as in that of Diporochaeta, or, finally, in the prostates, as in that of Woodwardia. If all such modifications occur, we shall obtain as a result a representative of the genus Megascolex. Such, Stephenson suggests (1921, p. 120), has been the course followed in the evolution of the genus Spenceriella. The genus consists of three species, one in India and two in Victoria, Australia ; there is nothing improbable in the supposition that they arose independently from the genera Megascolides or Diporochaeta, both of which inhabit India and Australia.

3. ITERATIVE FORMATION OF ALLIED FORMS

Koken (1902, p. 13) gave the name of "iterative formation of species" to the following phenomenon, which is observed to occur in the phylogeny of certain groups. Series of forms very similar, but possessing no direct genetic connection with one another, from time to time diverge from one common stem. Thus forms possessing a deepened lower valve and a flat upper one, and bearing the genetic name of Vola, have three times successively diverged from the molluscan stem Pecten : once in the Lias, the second time in the Cretaceous, and finally in the Oligocene ; in the intervals, Vola is absent (Philippi, 1899). A determined course in evolution is in this case displayed with exceeding clearness. Similar cases have been described in the Gastropoda (Koken), in the brachiopod Craniidae (Huene) and in the Crinoidea (Jäckel). The Cretaceous *Rhynchonella plicatilis* repeats the Palaeozoic type Uncinulus, *Rh. astieriana* the Triassic Halorella (Diener, 1910, p. 115).

Instances of iterative formation of genera in Foraminifera are described by Rhumbler (1913, p. 397): the polyphyletic genera Ammodiscus (known from the Silurian to the present time) and Spirillina (from the Cambrian to the present time) have arisen several times: from the genus Girvanella (Silurian—Recent) have several times branched off similar forms (which have developed in an identical or similar direction).

Palaeontology knows of other cases of the origin of similar forms, but not from a common stem. Thus, the cirripede crustacean Pyrgoma occurs in the Devonian and Tertiary deposits. True nummulites are known from the Jurassic and Tertiary, but are absent in the Cretaceous (Diener, p. 116).

We do not, of course, know what the structure of the soft parts of all these animals was; it is possible that their organisation, in spite of the similarity in their skeletal elements, was unlike. The case of the American terrestrial Mollusca, whose shells very much resemble those of the European Helicidae, but whose internal structure is perfectly distinct, shows the necessity for caution in this matter. But, in any case, even similarity in the shell alone clearly demonstrates a development in a parallel direction, and, after all, that is what interests us.

4. IS THE EVOLUTIONARY THEORY REFUTED BY THAT OF POLYPHYLETIC ORIGIN?

As we have seen (§ 1), Darwin believed that all animals have descended from, at most, four or five progenitors, and plants from an equal or lesser number. By analogy, he was even ready to conclude that all organic beings that have ever inhabited the earth have descended from one primary form, into which life may have been breathed by the Creator ("Origin of Species," chap. xv, p. 429). Monophyletic descent is supported by K. Schneider (1912) from quite

another point of view: every simple form contains *in potentia* a more complex one, the latter "evolving" from the former in the course of ontogeny and phylogeny. "Therefore," continues Schneider (p. 140), "there must exist some *one* primordial form, within which all the remaining forms are 'enfolded' (eingewickelt), all the morphological potentialities having already been contained in the primordial cell (Urzelle)." This is the point of view of pre-formation.

This is one extreme view. The other extreme was thus formulated by Linnaeus in his "Philosophia Botanica" in 1751: "Species tot numeramus, quot diversae formae in principio sunt creatae."[1] In 1758 Linnaeus, in the tenth edition of his "Systema Naturae," described 4162 species of animals; at the present time, over half a million of species are known, including fossils. In 1753 Linnaeus knew 5247 species of plants (Species plantarum). Now (1920) about 273,000 recent plants alone (of which 155,000 are angiosperms and 500 gymnosperms) are recorded.[2] In a word, Linnaeus when writing his celebrated aphorism did not know more than ten thousand species of plants and animals. In the present state of science, we may say that both Linnaeus and Darwin were in error, but that Linnaeus, from the purely quantitative side, was nearer the truth. To support the view that animals descended from four or five progenitors is now impossible: the number of the primal ancestors must be computed in thousands or tens of thousands.[3]

The absence of transitional forms between the larger, and sometimes the smaller, taxonomic units, the absence of ascertained cases of experimental production of new characters or genes (all the hitherto known and well-established

[1] It is interesting to note that five years earlier, in 1746, Maupertuis in his "Venus physique" was an advocate of monophyletic origin: "ce que nous reste à examiner, c'est comment d'un seul individu, il a pu naître tant d'espèces si différentes" (quoted after Bateson, 1913).

[2] Kuznetzov, 1922.

[3] Belogolovy (1911, p. 222) speaks even of "millions of initial points."

cases of heterogenesis (mutations) relate to the loss of genes or factors, and not to the production of new ones: regressive heterogenesis alone, and not progressive, is experimentally recorded), all this has caused some authors to assume a very pessimistic attitude towards the possibility of evolution in the form it was conceived by Darwin. Even before the resurrection of Mendelism, Zeiller, in his "Eléments de Paléobotanique" (1900, p. 382), said, "Au lieu de se transformer peu à peu les unes dans les autres, elles (les espèces) nous offrent en général une individualité bien accusée, demeurant fixes pendant tout le cours de leur existence, ou du moins ne variant qu'entre des limites déterminées et le plus souvent très resserrées. C'est ce qu'on remarque notamment dans la flore houillère, où cependant les documents ne manquent pas et où l'absence de formes de transition ne peut guère être imputée à l'insuffisance des matériaux recueillis: les espèces, comme les genres, se succèdent par voie de substitution et non par voie de transformation graduelle, et il parait être de même à tous les niveaux." Lotsy in a series of works (1912, 1913, 1914, 1916, 1917) advocates the opinion, that all the diversity of the vegetable world is a result of combinations of a certain number of permanent, non-varying, primary elements. There is no hereditary variability. Once constituted, the elementary species ("Jordanons") are constant. New species are produced by means of hybridisation: homozygous combinations at once give origin to new species, heterozygous produce such species in consequence of segregation. This view, in Lotsy's opinion, enables a parallel to be drawn between living and inorganic matter. Finally, Bateson likewise (1914, p. 640) inclines to the view that the entire process of evolution may be regarded as "an unpacking of an original complex which contained within itself the whole range of diversity which living things present." Thus also evolution is conceived by Davenport (1916).

As regards the views of Lotsy and Bateson we, with

Osborn (1915, p. 239), must say that they take no account whatever of palaeontology. I may add, that neither do they consider the data of biogeography. And yet these branches of science clearly show that the production of new genes (factors) actually occurs during the processes of the geological history and geographical distribution of specific complexes.

I imagine the process of evolution to have been the following. A large number, thousands and possibly tens *of thousands of primary germs, evolved more or less convergently* (parallel to each other). Some groups became extinct, others in supplanting them gave rise to new forms. Small taxonomic units (genera, species, sub-species) also originated divergently. Our point of view is thus intermediate between that of monophyletic origin, to which Darwin inclined, and that of absolute polyphyletic origin, which was at first maintained by Linnaeus and was subsequently advocated by Lotsy.

Convergent development is inconsistent with the principle of natural selection, for it is development based upon law, whereas natural selection is determined by chance. Hitherto it has been held that the organic world develops by means of divergence; similarities were alleged to be due to homology, *i.e.* to reciprocal consanguinity; convergence was regarded as a rare, accidental and external phenomenon, playing no essential part in the evolution of organisms.

But in very many groups of plants and animals we have shown above that the general trend of the evolutionary process is due to convergence, which affects not only the external, but also the most essential characters and organs of living beings. We have, it would seem, adduced a sufficient number of examples to support this view. Their number could easily be increased many times; but to exhaust the list of the phenomena of convergence, it would be necessary to make an exposition of the whole subject of the comparative morphology and anatomy of all plants and animals, both recent and fossil. For, we repeat, all development is determined

by laws, and is therefore subject to convergence: those organs are formed which must be produced in virtue of the constitution of the organism and the effect of external causes, and not any random forms, of which it is alleged only the best adapted will be selected.

Similarity in the organisation of two forms is not a sufficient reason for attributing to them a common origin; of course, similarity *may* be the result of an origin from common ancestors, but it *may* also be the consequence of a certain uniformity in the laws of Nature. The fact that rock-salt and diamond both crystallise in the isomorphic system affords no grounds for regarding these bodies as being genetically related or being derived from one common form.

To what conclusions may our consideration of the question of polyphyletic origin lead us?

It appears that this "vice," so strongly contaminating the purity of the phylogenetic tree, is an essential feature of the evolutionary process in animals and plants. Polyphyletic origin is characteristic not only of the larger groups, but of the smaller taxonomic units.

From the foregoing only one inference can be made. It is obvious that the method of the production of new forms, as advocated by Darwin, by means of the divergence of characters, is not accomplished in nature on the scale he supposed. The organic world develops on the whole convergently, not divergently, in a determined direction, and not in every direction. Polyphyletic origin, further, bears testimony to the absence of transitional forms between separate groups: however far we may penetrate into the history of a given group, it will never differ less from its neighbours; no common root is present; the differences are aboriginal, the similarities secondary. Both convergence and the absence of transitions support the view that evolution advances *by means of the transformation of vast numbers of individuals into new forms*, of which we shall treat more fully in the following chapter.

To illustrate the process of evolution in a graphic manner, it would have to be imagined, not as a growing tree, ever developing new branches, but in the shape of a book, each leaf (form) of which, on being turned over, would be replaced by the following one: the leaves, as they are turned over, sink into history, the open ones will live for a while.

CHAPTER X

THE FORMATION OF NEW SPECIES

THE doctrine of geographical landscape, which is one of the factors of the production of organic forms (Chap. VI), leads us straight to the question of the formation of species. From the foregoing it is evident that characters, typifying any given group, (1) either repeat what has been already possessed by the progenitors of that group, or (2) precede what will be accomplished in more highly organised groups (or is already possessed by them), or, lastly, (3) represent a distinguishing feature of the group. (From which it in no way follows that the characters of this latter class should not be convergently manifested, in some combination, in other groups.)

The repetition of *old* characters is based upon heredity, the precession of *future* characters is a result of the unfolding of existing rudiments. The production of *new forms* it will be more convenient to trace by studying the process of geographical isolation.

1. HOW DO NEW GEOGRAPHICAL FORMS ORIGINATE?

1. Have geographical forms (species, sub-species, "nationes"), like members of a family, descended from one single pair, or even from a single individual? In other words, are geographical forms monophyletic?

In the first edition of the "Origin of Species" Darwin inclined to such a supposition, admitting that an accidental favourable variation in one individual may have given rise

to a new species. But in subsequent editions of that book he had altered his point of view, and acknowledged that variations, which give rise to new species, should not be single ("Origin of Species," sixth edition, p. 72). In any case, according to Darwin, only *individual* variations play a part,[1] and only on *a few* of the inhabitants of the same region will natural selection act.[2]

Our opinion on this subject is that single and individual variations do not give rise to new forms.

In the origination of new geographical forms (species, sub-species, nationes) *a vast number of individuals inhabiting a certain geographical area are simultaneously involved in the production of new characters.*

There can be no question of an accidental occurrence of characters. Thus, *in the production of geographical forms natural selection plays no part.*

Let us illustrate the above by a few examples. The gudgeon (*Gobio gobio*) is widely distributed in Europe and Siberia. But in the South of Russia, in the Crimea, the Caucasus and Turkestan, as also in the North of Italy, the gudgeon displays variation in a determined direction: scales begin to appear in greater or lesser number on the throat, the body and caudal peduncle become deeper. In consequence, there appears a new sub-species, *lepidolaemus*, with its "nationes"[3] and other allied sub-species. The vast area occupied by this variation is remarkable.[4] The

[1] A great amount of variability, under which term individual differences are always included, will evidently be favourable (for the production of new forms through natural selection) ("Origin of Species," 6th ed., p. 80).

[2] *Ibidem*, p. 85. However, in a letter to Moritz Wagner, Darwin writes (on 13th October, 1876), "I believe that all the individuals of a species can be slowly modified within the same district, in nearly the same manner as man effects, by what I have called the process of unconscious selection" ("Life and Letters," iii, p. 159). On "unconscious selection" see "Origin of Species," p. 80.

[3] See my "Poissons" in "Faune de la Russie," iii, p. 2, 1914, pp. 422-461.

[4] The northern gudgeon, *G. gobio* typ., may actually have been derived from southern forms. *But this does not alter the substance of the matter* under discussion.

same is true of a kind of bleak (*Alburnoides bipunctatus*), and probably will be found to apply to most fishes, when they have been thoroughly studied from a geographical point of view.

Here also, selective mortality could be appealed to as a probable explanation: it may be urged that all gudgeons with a naked throat become extinct in the south. But the fact remains that such an explanation, purely hypothetical,[1] fails to clear up the matter. The trend towards the development of scales on the throat, united with a combination of other characters, is something *primary, occurring in accordance with some law throughout the entire area of distribution of the southern gudgeon*. Selection is confronted with a developed tendency, and not with chaotic, accidental characters, occurring without the intervention of any law. The adherents of selection regard accordance with law as a result of selection; we, on the other hand, have shown in the preceding chapter of this book that accordance with law, *i.e.* a determined tendency, exists as something primordial, effected without any intervention on the part of selection, and prior to its being able to exert its influence.

In foregoing chapters we have shown how great is the effect of the geographical *landscape*; it affects all, or, at least, a preponderating majority of individuals inhabiting a definite geographical area. As an example, we may recall the darkened colouring observed to occur in many South European forms (p. 266). It is perfectly obvious that such a colouring could not have occurred as a consequence of single variations. It is a *new character*, which has affected the entire mass of southern individuals of a given form. Those melanistic varieties, which have recently been observed in the moths of Europe (*Amphidasys betularia*

[1] It may also be mentioned that the occurrence of scales on the throat of the gudgeon, even in a rudimentary condition, has *never* been observed in the north.

aberr. *doubledayaria* may serve as an example), are, on the contrary, single variations. As a result of crossing of the typical with the geographical form, or of one sub-species with another, intermediate hybrids are obtained, as usually happens when Linnaean species are crossed, and in the offspring little or no segregation is observed. And yet, when morphas and aberrations are crossed with the typical form, or elementary species (" Jordanons ") with one another, alternative segregation is observed (when crossing *betularia* with *doubledayaria*, a generation consisting of *betularia* and *doubledayaria* is again produced (Gerschler, 1915)).[1] The same has been clearly shown by the experiments of Standfuss (1896). He, for instance, crossed the male of the butterfly *Callimorpha dominula* L., widely distributed in Europe, with the female of the sub-species *persona*, which inhabits Italy, and, reciprocally the male of the latter with the female of the former. Forms intermediate between the two were obtained. The same results occurred after the crossing of other species with their sub-species. Sumner (1920) has also shown this in his crossing experiments with the rodent Peromyscus. And yet, after the crossing of the typical species with the aberrations of the same species, in the offspring the typical species and its aberration were obtained, and not an intermediate form.[2]

Geographical forms are apparently the result of the effects of external agencies, *i.e.* of the landscape, whereas the non-geographical ones are due to internal causes. That being so, it is understandable why sub-species and " nationes " should inhabit a continuous area : the effects of the landscape would at once tell on a vast number of individuals.

[1] This is, apparently, not always the case with elementary species. Thus, according to the observations of Rosen, intermediate forms were obtained as a result of the inter-crossing of the elementary species of *Erophila verna*.

[2] This is clearly stated by Standfuss.

We have mentioned above that in the formation of sub-species a vast number of individuals is subject to transformation. It is sometimes true of *all the individuals*; but it not *infrequently* occurs that the new character is *exhibited in a considerable number*, being absent in other representatives of the group inhabiting the same area. Thus, in the typical roach there usually are 45 scales in the lateral line, in its Lower Volga sub-species, the serushka, there are 43, in the vobla 44; but the limits of variation in the number of scales are as follows (Pravdin, 1915, p. 64):—

Roach (*Rutilus rutilus rutilus*), 43-46; 45 scales in 48%, 44 in 37%.
Serushka (*R. r. fluviatilis*), 42-45; 43 scales in 50%.
Vobla (*R. r. caspicus*), 42-47; 44 scales in 38%, 43 in 34%.

In the European dace (*Leuciscus leuciscus leuciscus*) the anal fin usually has 8 branched rays (limits of variation 7-9), in its Siberian sub-species (*L. l. baicalensis*) usually 9 (limits of variation 8-11).[1] The character varies gradually as we pass from the area of the distribution of the maternal form to that of the sub-species.

The foregoing, however, in no way invalidates our principle, that in the process of the geographical production of forms vast numbers of individuals are affected: the mean *standard* of the complex is modified.

On the mode of formation of sub-species, Russian botanists have advocated opinions analogous to those mentioned above. Komarov (1901, p. 84), in his "Flora of Manchuria," says that the formation of new sub-species or "races," as he calls them, is only on very few occasions due to individual variations. "For the origin of a new race it is necessary that its typical features should at once be manifested in a number of individuals, or, truer still, in all the individuals inhabiting a given geographical area." As

[1] See Berg, 1912, pp. 103, 110.

Komarov justly observes, this happens whenever, for instance, a change of the climate occurs. "Such a change affects all the inhabitants of a given locality, it destroys some, transforms others, and, lastly, presents conditions favourable for the immigration of new-comers from neighbouring districts." "The genesis of new races (or sub-species in our terminology, L.B.) consists in transformation of entire generations due to the agency of physico-geographical conditions: the variations of the former follow those of the latter on parallel lines and quite as prominently." "The formation of new races (*i.e.* sub-species, L.B.) conforms to the secular modifications of climate and other conditions essential to the welfare of plants; in its essence it is a slow and to us imperceptible transmutation of the physiological activities of the organism involving a gradual, but radical transformation of its morphological structure" (p. 85).

This opinion is shared by Paczoski. This eminent botanist does not agree with the widespread view that species originate in one spot, and subsequently extend the area of their distribution by means of migration; a new sub-species arises under the effect of general causes over a considerable, or even over the whole, area occupied by the segregating maternal sub-species (1910, pp. v-vi; 1914, p. xxvi *seq.*).

The phenomenon alluded to, the "epidemical" character of the formation of species, the simultaneous *en masse* manifestation of new characters over a vast territory, is a matter of the greatest importance in the problem of evolution. According to the views of the adherents of natural selection, of a vast number of individuals only a few succeed in rising to a higher position through the struggle for existence (Plate, "Selektionsprinzip," 1913, pp. 512, 604); we assume, on the contrary, that the formation of species affects vast numbers of individuals. We lay particular stress on this point, since Darwin, in chap. iv of the "Origin of Species" (pp. 84-85), says, "But I do believe that

natural selection will generally act very slowly, only at long intervals of time, and *only on a few of the inhabitants of the same region.*" [1]

Had variation failed to affect simultaneously a vast multitude of individuals, it would, from the point of view of selection, very generally possess no value. Thus, it is advantageous for bees to possess a long proboscis, as in that case they are able to suck honey from the flowers of clover. *But a modification in the line of increasing the length of the proboscis would have to affect a multitude of individuals, for, operating on individual variability alone, selection could lead to no progress.* Let us illustrate this by an example. Khokhlov (1916, p. 23) measured the length of the proboscis in 1800 Russian bees, belonging to six races. On a descending scale in the length of the proboscis these races may be arranged in the following order—Abkhaz (6·73 mm.), Kars, Carniola, Ukraine, Italian, Orel (6·28 mm.). The mean length of the proboscis in the Abkhaz bee is 6·73 mm., with limits of variation 7·15 and 6·33 mm. Bees provided with a proboscis 7·15 mm. long, of course possess an advantage in the struggle for life, but, as regards the welfare of the hive, this is fully set off by unfavourable variations in the opposite direction, viz. in 300 Abkhaz bees the maximum length of the proboscis appeared in two cases and the minimum in as many. Thus, in operating upon individual variability, selection cannot produce anything new. The race will secure a decided advantage only when the increase in length occurs in a large number of individuals, more than a half. But that would be variation in a determined direction, whence the element of chance is eliminated. This circumstance, *i.e.* a simultaneous variation

[1] But, on the other hand, in "Variation of Animals and Plants" (chap. xx, p. 192), he says, "In separated districts, long-continued exposure to different conditions of life may perhaps produce new races without the aid of selection." (Compare also chap. xxiii, p. 271.) By the time that work was published, Darwin had considerably modified his views on the part played by selection (see above, chap. i.)

in the length of the proboscis in a mass of individuals, may actually be observed in another geographical region, Abkhasia, Caucasus. For some reasons, the conditions are here more favourable than in the Government of Orel (Central Russia) for the increase in the length of the proboscis in the bee, and the phenomenon occurs *in the mass*: the prevailing length of the proboscis in the Abkhaz bee is 6·60-6·90 mm., whereas in the Orel bee it is only 6·16-6·38 mm. Red clover can be profitably visited by bees with a proboscis not less than 6·70 mm. in length; now, the Abkhaz race numbers 61% of such bees, while the Orel race has no more than 1·3% (Khokhlov, p. 31).

2. That in the formation of species a large number of individuals are simultaneously affected becomes clear when the results of the operation of selection are considered. We have shown above (p. 64) that the part played by selection consists in the *maintenance of the standard.* Therefore, variation may occur only when the *standard, i.e.* the average value of characters of a "population," varies. Yet, in the opinion of Darwin, the principle of the divergence of characters "will generally lead to the most different or divergent variations being preserved and accumulated by natural selection." "A set of animals, with their organisation but little diversified, could hardly compete with a set more perfectly diversified in structure" ("Origin of Species," chap. iv, p. 90).

In proof of the conservative tendency in natural selection we may offer a few more examples.

J. A. Harris (1913, p. 683) investigated the mortality of a large number of seeds of the kidney-bean (*Phaseolus vulgaris*) under field cultivation, and found that the heaviest and the lightest seeds were the most liable to succumb. The seeds of medium weight survive best. The mean weight of a large number of seeds which had survived does not differ from that of the series from which they were taken; but the variability of the surviving seeds is less. The large and

small seeds are less liable to develop into seedlings than those of normal weight.[1]

Considerations such as the above lead us to conclude that the best chances of surviving fall to the lot of those *which approach the standard*, and not those which deviate from it.[2] This circumstance is connected with the principles of convergence of characters and of "epidemical" mutational variability, of which we have already spoken: whenever variations occur in accordance with law, and not by chance, they should be manifested in a vast majority of individuals; but if variations do not ensue, if the time for change has not yet come, the rare individuals which are modified are doomed to perish; the remaining mass of organisms will not follow their example.

In proof of the effectiveness of natural selection, the observations of Bumpus (1899) on sparrows are often adduced. During a storm in New England 136 sparrows perished, and were then subjected to a detailed examination as regards variability. On being compared with the sparrows of that locality, it was found that the victims of the storm were just those sparrows which differed most from the average typical local sparrow in having tails, wings and bills longer or shorter than the average. Those sparrows which had least departed from the standard, says Plate ("Selektionsprinzip," p. 184), survived.

But it is just in a case like this that the principle of selection is best refuted. It might have been expected that the survivors in the struggle for existence would be the individuals which deviated most from the standard; for some or any of these deviations might have proved by chance to be useful. By such means the foundation for the production of a new form might have been laid down. But it appears that such is not the case: in this example, the best-adapted

[1] It must be noted, however, that in certain series of beans (1913, p. 758) the less liable to develop were large-sized beans, and in others small-sized ones.

[2] On this subject compare also K. C. Schneider, 1911, pp. 95, 106, 111-112.

sparrows were the vast mass of *average* individuals. Hence it is perfectly plain that the best-adapted cannot be sifted out by selection, as they are already present in the vast majority of individuals.

Thus if a useful character or contrivance is to have any chance of being preserved, it should be simultaneously manifested in a *vast number of individuals* ; such individuals would be the most resistant to unfavourable conditions, and the extreme deviations would perish.

The facts obtained by Bumpus are not exceptional. Crampton (1904) measured 1090 pupae of the moth *Philosamia cynthia*, collected in New York in December, 1899. Some of them perished, the remainder produced moths. It then appeared that the pupae that had perished were those which had deviated most from the standard. This case is particularly interesting from the fact that the pupae are unable to make active use of their organs.[1]

> We may also remind the reader of the modification in the shape of the skull, due to novel geographical conditions, to which are subject in the mass descendants of Jews and Sicilians who have emigrated to America ; let us refer also to the experiments on *Zoarces vivipara* (see Chapter VI, § 3).

In short, selection is a factor preserving the standard and limiting variation. It cannot, therefore, be an agency for the production of new forms. If that be so, geographical forms cannot be produced except in the mass.

Darwin himself, with his habitual conscientiousness, remarks that instances occur when all (or a part of) the individuals of the same species have been similarly (*i.e.* in one direction) modified " without the aid of any form of selection " (" Origin of Species, chap. iv, p. 72). The cause is attributed by Darwin to the fact that the members of the same class " have inherited so much in common in their constitution, that they are apt to vary under similar exciting

[1] Quoted from Przibram, iii, p. 213.

causes in a similar manner" ("Origin of Species," chap. xiv, p. 375, and "Variation of Animals and Plants," chap. xxiii., pp. 271, 272).

If any new originating form (variety, according to Darwin) be represented, as Darwin assumes, by a single individual or a small number of the latter, it will, in the course of intercrossing, dissolve in the general mass of the parental form. Of course, it cannot entirely vanish, for whenever a new character becomes hereditary, and if we have to do with a variety (not a species), an alternative or Mendelian inheritance ensues. Plate ("Vererbungslehre," pp. 445-446) takes the following example. Let there be six black mice freely intercrossing with each other only; two homozygous males and as many females, one heterozygous male and one heterozygous female. From all possible combinations of crossing, we shall obtain ten heterozygous black and one homozygous white to twenty-five homozygous black individuals. The same relative proportion will be retained in all subsequent generations.[1] Plate himself comes to the pessimistic conclusion, that "if the new race is unendowed with some advantageous features in structure, it can never become dominant, while being represented but by a few separate individuals." Yet Plate took a case in which one-third of the individuals were subject to modification, whereas, according to Darwin, one-hundredth or one-thousandth fraction of one per cent. would be sufficient for that purpose. To save the hypothesis of natural selection, Plate was induced to find recourse to the principle of "geographical, biological and sexual isolation."

The following inference may therefore be made: a new form will be dominant, if it becomes so *immediately* on its

[1] The case would be somewhat more favourable had the maternal form been recessive and the mutant dominant. But even then, under the same favourable conditions as those offered in the case suggested by Plate, to twenty-five maternal (recessive) individuals there would be ten *DR* and one DD. But we must repeat, the frequency of new variations is too much exaggerated in comparison with what is demanded by the theory of selection.

initiation. This is but another way of expressing our view, *i.e.* that new forms originate " epidemically."

2. NEW FORMATIONS IN LANGUAGES

The mode of origin of new forms characteristic of subspecies is applicable to languages. New forms here also arise simultaneously in vast groups of individuals; single variations, on the other hand, disappear with the death of the individual in whom they sprang up. Every peculiarity of speech typical of a dialect, is simultaneously and independently displayed by all the children of a given territory. This circumstance may account for the wonderful uniformity of the phonetic principle, and in part, for that of the morphology manifested in an overwhelming majority of individuals comprising a linguistic unit. Thus, the Russian language is characterised throughout the entire territorial extent of its distribution by its full-sounded combinations *oro, olo, ere, elo*; in South Slavonic and in the Tchekh-Slovak languages these combinations are invariably supplanted by *ra, la, rě, lě* respectively; while in Polish and other West Slavonic languages they are as rigidly represented by the sounds *ro, lo, rze, le.* For instance, to the Russian *vorona* (crow) correspond the old Bulgarian *vrana* and the Polish *wrona.*[1] The Southern Great Russian dialect is distinguished from that of the North and from Little Russian by the written letter *o* being pronounced as *a*; this use is a very old one, dating from the period when the East Russians in the basin of the Oka and of the Upper Volga had not yet come into close contact with the North Russians, and before the White Russian dialect, in which the same peculiarity occurs, had diverged as a separate branch from the common stem (*i.e.* before the thirteenth century).[2] It can hardly be assumed that the peculiarity mentioned had developed in

[1] The examples are borrowed from Shakhmatov (Schachmatow), 1916, p. 19.
[2] *Ibidem*, pp. 53-54.

one centre, subsequently spreading throughout the entire population of the Southern Great Russian.[1] It seems much more probable that it had simultaneously affected a vast group of the Russian population. Another vocal phenomenon, which well accords with this supposition and is characteristic of the entire Russian language, is the decline of the surds Ъ and Ь, their complete disappearance in some cases, and conversion into *o* and *e* respectively in others; this occurred in the second half of the twelfth century and, possibly, in the first decades of the thirteenth *simultaneously throughout the whole territory occupied by Russian dialects.*[2] At about the same time, in the twelfth or thirteenth centuries, the use was lost of the dual number, instrumental local case, declension and genders in the comparative degree of adjectives and participles, aorist, imperfect and pluperfect tenses, optative mood, etc. In a word, a recoinage or a recasting, as it were, of the Russian language was simultaneously effected over a vast territory. Soon afterwards, in the end of the thirteenth or beginning of the fourteenth century, the new Great Russian nationality began to be formed.

Similarly, in the fifteenth century the sound *sh* was lost in Spanish, being universally replaced by the strongly aspirated *h* (Spanish *j*).

In support of our argument we may appeal to the authority of a leading French linguist, Meillet (Russ. ed., 1911, p. 22).[3] "Innovations occur," he says, "which have deep-rooted causes and which are displayed by *all children*,[4] born of native parents throughout a definite period of time. From a given moment, *all children*[4] born in the same locality, acquire a certain articulation of speech, differing from that

[1] Shakhmatov (1916, pp. 83-84) holds a different opinion: variations in language originate in separate individuals and the spread of these novel forms is subject to "the response they find in the psychical and psycho-physical nature of the surrounding linguistic medium."

[2] Shakhmatov, pp. 84-85.

[3] L. V. Bianchi drew my attention to his book.

[4] The italics are mine.

of the adults, which they are no longer able to reproduce." Thus, at a certain period, children in the north of France began to pronounce *y* (*l mouillé*) instead of *l*; as in "ll" of the word *vaillant*, which they pronounced *vayant* instead of *vailant*. This pronunciation has spread all over the north of France, but there are some localities where people born at about 1850 can still pronounce the *l*, although the younger generation has lost that usage. Another example is afforded by the inhabitants of ancient Attica, where the use of the dual number lasted till the end of the fifth century B.C.; but the authors who were born between 440 and 425 B.C., such as Plato and Xenophon, began to show a certain hesitancy in its use, after which the dual number completely disappears. "Variations of such a kind, being common to *all generations commencing from a definite time*,[1] are transmitted to younger generations; they thus accumulate and, in proportion to the rapidity with which they spread, modify the language in a more or less considerable period of time." "They are due," says the French linguist, "not to any desire for change; on the contrary, they arise in spite of the efforts faithfully to reproduce the language of adults."

As in animals and plants, so also in languages, new formations rapidly succeed each other in some complexes (species, languages), while in others characters are more stable, or, as is stated by Meillet, "a series of generations may preserve the same speech practically intact."

We cannot resist the pleasure of quoting the following passage from the work alluded to, where the parallelism in the development of language and the formation of species in organisms, as we understand the latter in this book, is set forth with unusual lucidity. After having presented the facts from the history of language, just mentioned, Meillet continues (p. 23), "Such is the normal type of the evolution of a language. It is the result of the natural continuity of generations and of the identity in the aspirations and faculties of the numbers of

[1] The italics are mine.

a given generation at a given period. Although variations of this type *independently occur in every dialect of a given locality*,[1] we must not lose sight of the fact that they take place *in different, although adjacent moments of time with inconsiderable deviations in all places inhabited by a generally homogeneous population* [1] speaking the same language and living under similar conditions. Thus, the *l* was converted into *l mouillé* in the entire north of France, the Greek dual number had already disappeared in prehistoric times in the Æolic dialect, in the Ionic of Asia Minor and the Doric of Crete, and in the fourth century B.C. in the Attic, in the Doric of Laconia, in Boeotic and Delphic, *i.e.* in the cities of continental Greece." "*The causes of such variations, generally unknown, are not particular to one locality, but operate in extensive regions.*" [1]

In my opinion, the above-mentioned variations of language are determined by *modifications in the organs of speech*, *i.e.* possess an anatomical basis. These phenomena, consequently, enter into the domain of the naturalist: they are fully homologous to the new formations to which the various forms of organisms have been subject in time (geologically) and in space (geographically).

3. HETEROGENEOUS VARIATIONS, OR THE MUTATIONS OF DE VRIES

We must now consider the question, whether new forms are not produced by the method that was called by Koelliker (1864) *saltatory variation* (sprungweise Veränderungen), and by Darwin (1868, "Variation of Animals and Plants," chap. xi, p. 373) *bud-variation* or "*sports*," by Danilevsky (1885, pt. i, pp. 401-411) *sudden spontaneous variations*, by Korschinsky (1899) *heterogeneous variations*, and by de Vries (1901) *mutations*.

An example of mutations may be offered by the single leaved strawberry, *Fragaria monophylla*, a new "species," suddenly obtained by Duchesne in 1761 from the seeds of

[1] The italics are mine.

the common European wild strawberry, *Fragaria vesca,* and which proved to be constant. This case was mentioned by Darwin (*l.c.*, chap. x, pp. 352-353), Danilevsky (p. 406), Korschinsky (pp. 8-9) and de Vries (1901, p. 136, fig.; 1906, p. 365, fig.).

We shall not here discuss the question whether new forms are produced by means of the accumulations of slow, gradual variations, as is generally assumed to be the case,[1] or by sudden leaps, as is advocated by de Vries. We shall only refer to the quantitative relations, in which the mutations of de Vries are exemplified. And this will enable us to solve the question whether new characters are produced in nature by means of heterogeneous variations.

As a rule, mutations are displayed in a very small number of individuals. "I am quite unaware," says Korschinsky (1901), "of any fully reliable and exact observations, which refer to the occurrence of any heterogeneous variations in more than one individual simultaneously." Heterogeneous variations are not infrequent in cultivation; they are generally preserved in that case. Wild plants also produce variations, but these usually become extinct (p. 78). But even amongst cultivated plants mutations not infrequently either do not blossom (*e.g. Broussonetia papyrifera* var. *dissecta*), or do so rarely and sparingly, or, lastly, if they do blossom, produce no seeds or only very few (p. 82).

In the experiments of de Vries (1901, pp. 157, 178) on 53,500 individuals of *Oenothera lamarckiana*, mutations were manifested in 834, or 1½%, of the individuals examined, a most insignificant quantity. Seven forms of mutants in all were obtained, and the number of individuals in each never exceeded 2% of the amount of *Oe. lamarckiana* sown.[2]

[1] Among palaeontologists this view is chiefly insisted upon by Osborn, 1912, 1915.

[2] I am therefore unable to understand why de Vries' statement (1901, p. 177; 1906, p. 346), "New species arise in a large number of individuals" should be included among his "laws of mutation." This thesis,

This, then, is evidently not the manner in which new hereditary forms are produced in a state of nature, where in the formation of a species a vast number of individuals is simultaneously affected.

De Vries himself observes (1906, p. 344) that among natural elementary species, such as Draba (Erophila), it is impossible to detect any maternal form which would, like *Oenothera lamarckiana*, give rise to other species: in that case the quantitative proportion of different elementary species is fairly equal. May it be concluded therefrom, asks de Vries, that the initial form of Draba is extinct? Or is it concealed under a number of other forms of Draba? "Had our mutants *Oenothera gigas* and *Oe. rubrinervis* grown in a wild state *in equal numbers* [1] with *Oe. lamarckiana*, would it then have been possible to determine which of them had produced the others?" In equal numbers! That contains the whole pith of the matter.

The mutations of the snap-dragon (Antirrhinum) and of the fly Drosophila, both following Mendel's law in respect of one factor, also appear in a very small number of individuals: in Baur's experiments, among 1000 seedlings of Antirrhinum, 2% of heterozygous, and only 0·5% of homozygous, mutations were found.

De Vries says (1901, p. 178; 1906, p. 349) that the mutations he was able to obtain from *Oenothera lamarckiana* have no determined direction: they are produced in a promiscuous manner. Some of them are stronger (*Oe. gigas*), some weaker (*Oe. albida*) than the parental form; some have broader leaves (*lata*), others narrow (*oblonga*); some have larger flowers (*gigas*), others of a more intense yellow (*rubrinervis*), (the third smaller flowers (*scintillans*), the fourth paler ones (*albida*)); the capsule may be longer (*rubrinervis*)

with which I agree in principle, does not at all follow from his experiments on Oenothera. It is necessary, however, to note, that in the subsequent experiments of Bartlett (1915) on *Oe. praticola* 499 plants out of 500 were subject to mutation.

[1] The italics are mine.

or broader (*gigas*), or more rounded (*lata*), or smaller (*oblonga*), or unprovided with seeds (*brevistylis*); *rubrinervis* has a tendency to become an annual, *gigas* a biennial (p. 351), etc. "If in order to assure the appearance of one useful new character, nature is compelled simultaneously to produce ten, twenty, or more ineffectual (mutations), its ability to perfect by means of pure chance must be conceded," says de Vries (1906, p. 430).[1]

Yet the variations that give rise to new forms capable of surviving, as we have shown in the preceding chapter, evolve in a determined direction.

It is now practically established that the mutations that have been observed by de Vries to occur in *Oenothera lamarckiana* are the result of the hybrid nature of the plant. At least Davis (1916), by crossing *Oe. biennis* and *Oe. franciscana*, succeeded in obtaining a hybrid (*Oe. neo-lamarckiana*) extremely like *Oe. lamarckiana*. The latter species does not belong and did not belong to the American flora; it first became known in 1797, when it was described in Paris from specimens grown in the Botanical Garden of the Muséum d'Histoire Naturelle. To the same conclusion lead the results of the Mendelian analysis of the offspring of crosses of *Oe. lamarckiana* (Renner, 1917, 1919; Müller, 1918).

In general, the subject of the "mutations" of *Oenothera lamarckiana* has proved to be much more complicated than was thought by de Vries in 1901-3, when he published his "Mutationstheorie."[2] At present there can be no doubt that *Oe. lamarckiana* is a *heterozygous* form. But it cannot be called a hybrid of the usual Mendelian type: the products of its segregation are so-called "mutants."

[1] In a subsequent work (1912) de Vries, supporting his views as to mutations, as variations possessing no definite direction in evolution, tentatively puts forward the suggestion, that the elimination of unfavourable mutations by selection may give the impression that mutations follow a determined course. Cf. also "Mutationstheorie," i, 1901, p. 144.

[2] Cf. for instance, what de Vries says on the mutations of Oenothera in 1912 in "Die Mutationen in der Erblichkeitslehre."

De Vries himself, as early as 1903 (ii, p. 504), considered, that *Oe. lamarckiana* is a "semi-mutant" produced from crossing a gamete that had undergone mutation with one that had not. From such a combination proceeds a heterozygous form, which nevertheless seems to be constant. The remarkable observations of Renner (1916) led him to the conclusion that *Oe. lamarckiana* produces two kinds of gametes, one of which he calls *velans*, the other *gaudens*. By means of self-fertilisation *Oe. lam.* may produce the following combinations: *gaudens* × *gaudens*, (2 ×) *gaudens* × *velans*, *velans* × *velans*.

Of these the homozygous combinations (*gaudens* × *gaudens* and *velans* × *velans*) succumb; only the heterozygous, *gaudens* × *velans*, survive, which produce what is called *Oe. lamarckiana*. That this is so is proved, among other things, by the circumstance that 50% of the seeds of *Oe. lamarckiana* are not viable. Thus, the "constancy" of *Oe. lamarckiana* is only apparent, being due to the extinction of the homozygous combinations; therefore it is incorrect to describe *Oe. lamarckiana* as "a constant hybrid" (de Vries) in distinction from Mendelian hybrids. But obviously neither is it the usual Mendelian hybrid, for, as has been remarked by Lotsy (1917, p. 328), the gametes which had given rise to the "hybrid" are the same that belonged to the parental forms. Heribert Nilsson, Renner and Müller (1918) regard *Oe. lamarckiana* as a complex hybrid of the Mendelian type. Müller, considering the analogy to the fly *Drosophila*, admits the operation of the "lethal" factors, as also the interchange between chromosomes (crossing over). Lotsy (1917, p. 330), on the contrary, suggests that *Oe. lamarckiana* is not a true, but, as it were, a graft hybrid (*i.e.* somewhat of the nature of *Cytisus adami;* see above, Chap. I), in which, however, the fusion of the nuclei of both components has taken place. Lotsy looks upon *Oe. lamarckiana* as a *nuclear chimæra* (it approximately corresponds to *Solanum darwinianum*). Both components of its nucleus behave independently and give

origin to the very gametes by which they are produced. As is known, it has become possible to obtain *Oe. lamarckiana* from its components: by crossing *Oe. biennis* with *Oe. lamarckiana* two constant forms, *Oe. laeta* and *Oe. velutina*, have been produced; in crossing *laeta* with *velutina*, *lamarckiana* may again be obtained. Moreover, *laeta* and *velutina* are obtained as products of segregation from crossing not only *biennis* with *lamarckiana*, but also *muricata* with *lamarckiana*; from these last—*laeta* and *velutina*—*lamarckiana* may also be reproduced.

Some of the mutants of *Oe. lamarckiana* behave like *Oe. lamarckiana* itself, and may also be called *nuclear* chimæras.

Lotsy has suggested that, generally speaking, the occurrence of mutations is a consequence of the heterozygous character of the initial forms. Possibly such is the case.

Further, de Vries investigated about one hundred species in relation to their capacity for mutation. The result was negative, as only in *Oe. lamarckiana* were mutations manifested. Hence it is clear that *Oe. lamarckiana* is quite an exceptional form. De Vries supposes (i, 1901, p. 151) that of all the plants of the locality which were investigated, *Oe. lamarckiana* alone is in a period of mutations.

Finally, Heribert Nilsson, as early as 1912, showed that the mutants of *Oe. lamarckiana* are *not constant*: some give rise to the maternal form, others to other mutants. Thus *leptocarpa* produces *nanella*; *nanella*—*oblonga*; *oblonga*—*albida*, *elliptica* and *rubrinervis*; *scintillans* produces *lamarckiana*, *lata*, *nanella* and *oblonga*, etc. This proves that the mutants of de Vries are not always constant; some of them segregate. Nilsson comes to the conclusion that in the mutations of *Oe. lamarckiana* we encounter phenomena of a complex recombination of characters, *which were present in the initial form*.

Lately it has been found, as has been pointed out by Goldschmidt (1923), that some mutants, after a certain

time, return to the condition of the initial form by means of reversed mutation. In the case of Datura it has been shown by the experiments of Blakeslee that reversion is even effected by vegetative means.

The mutants of the fly Drosophila are for the major part much less viable than the maternal (initial) form, and the greater the mutational leap the lower is the viability of mutants. Of dominant mutants, *i.e.* not more than about 10%, the majority is generally non-viable in the homozygous state, and even the majority of recessive mutants also appears to be little adapted for the struggle for life. These facts, says Goldschmidt (1923), show that, generally speaking, *mutation is a modification* of the *gene in an abnormal* direction. The probability of obtaining a viable gene by means of mutation is generally very slight.

From the foregoing it is clear that neither individual hereditary variations such as the mutations of Oenothera, nor the similar mutations, following Mendel's law, of the type of Antirrhinum or Drosophila, nor, still less, individual non-hereditary forms (fluctuations), can give rise to *new* forms ("nationes," sub-species, species). For the production of new stable forms a transformation *en masse* of the entire or of the major part of a complex of individuals occupying a definite territory is requisite: only in that case will variation be firmly fixed by heredity.[1]

A transformation of forms *en masse*, so far as we know, occurs under two conditions. *Firstly*, when geographical environment is changed in space, *i.e.* when forms are geographically isolated, this being a *choronomic* process. As an illustration we may refer to the case of the Abies of Eastern Asia. In the forests of Manchuria and in the South of the Okhotsk region occurs *Abies nephrolepis*; in Japan, Hondo, *A. veitchii*; in Sakhalin and Yezo, *A. sachalinensis*; in

[1] We repeat, we are not discussing the question whether new forms originate gradually or by saltation. We are concerned with mutations from the point of view of the *quantity* in which they appear in nature.

Kamchatka, *A. gracilis*. All these species, according to Komarov (1901, p. 215), once constituted a single one. *Secondly*, in response to *autonomic* causes, when variations are manifested in the passage from one geological stratum to another. The above-mentioned series of Paludinas (Chap. II, § 3) may be taken as a corroborating example. To this subject we shall now turn.

4. MUTATIONS OF WAAGEN

The palaeontologist Waagen (1869, p. 186), starting from his researches on the Jurassic ammonite *Oppelia subradiata*, was the first to establish the conception of *mutations* ; he determined the differences subsisting between his mutations and what we now call sub-species. (We may remark that the mutations of Waagen have nothing in common with those of de Vries.) Waagen maintains that varieties, which are designated by botanists and zoologists as "local," "geographical," "space-varieties," are transient forms, confined to a definite geological horizon and not occurring in the higher (or more recent) horizons ; they possess but secondary systematic importance. In distinction from geographical varieties, mutations are transformations of the *species, occurring in time, during the transition from one* geological stratum to another. They are constant.

An ascending series of mutations in a succession of horizons is a *collective species* according to Waagen (=Formenreihe of Beyrich=phylum of many recent palaeontologists).

What Waagen calls a mutation is apparently due to internal (autonomic) causes alone. This opinion was held by Waagen himself : he attributes the origin of mutations to a "law inherent in the organism" (p. 239), and points out that such a conception differs from that of Darwin. Waagen derives his opinion from the fact that the various parts of Europe, where the same mutations had been observed,

could not have possessed the same physical conditions, although the forms produced are identical.

"Geographical varieties" or sub-species, on the contrary, are due to the effects of external geographical agencies alone.

Such are the differences between the mutations of Waagen and sub-species. The features common to both are (1) the transformation *en masse*, and (2) development in a determined direction.

That a transformation of a vast number is required for the occurrence of the mutations of Waagen may be seen from the following remarkable observation of Neumayr. In ammonites of the series *Phylloceras heterophyllum*, an ever-growing complexity of the lobate line is exhibited as we proceed from more ancient to more recent deposits; in this an evolution in a determined direction is manifested. *At the same time, amongst specimens of the same species* occurring simultaneously, extremely few individual variations are displayed. "I have long studied the Phylloceratidae with the greatest care," says Neumayr (1889, pp. 59-60); "through my hands have passed more specimens of this group than has ever fallen to the lot of any other palaeontologist; and I have come to the conclusion that few other forms could be found which possess such *minute differences between simultaneously occurring individuals of the various species*; if differences occur, they refer to any features rather than to the lobate line. And yet the lobate line radically varies in successive strata."

This was written by Neumayr. We evidently do not encounter variations in the lobate line in contemporary deposits, because they affect a *vast number* of individuals simultaneously.

Like Waagen, Neumayr (p. 60) is of the opinion that the formation of sub-species essentially differs from that of mutations.[1]

[1] Similarly, the well-known zoogeographer Ortmann (1896, "On Separation," p. 63; "Grundzüge," pp. 31-32) thinks that, by means of

Neither in the production of the mutations of Waagen, nor in that of geographical forms (species, sub-species, "nationes") does selection play any part, for both transmutations (1) simultaneously affect a vast number of individuals and (2) proceed in a determined direction; and both of these are inconsistent with the principle of the *selection of chance variations.*

The mutational production of forms proceeds periodically, i.e. is saltatory. There are periods when the creative power of nature is displayed in an inexhaustible kaleidoscope of organic forms, and others when it does its routine work, or, so to speak, slumbers. The division into eras, periods or epochs is, indeed, an external manifestation of this. The major sub-divisions correspond to *sharp* alterations in fauna and flora. But, on the other hand, we have a minute subdivision of the Jurassic into zones, to each of which corresponds its particular species of ammonite: in such periods the formative work of nature proceeded at a calmer rate.

The foregoing mutational theory of the formation of species accounts for several phenomena which have hitherto been enigmatic. Such were (1) *the polyphyletic origin* both of small and of large groups. (Its cause is displayed in the very manner in which new forms are produced, which is polyphyletic, and is accomplished by means of the *transformation of vast numbers of individuals or of all the* components of the species); (2) *the sudden appearance of species*; (3) *the absence of transitions between species.* Species arise either (*a*) through a geological, mutational transformation, embracing the entire mass of individuals or a large area occupied by the given species, or else (*b*) through geographical isolation. If in the latter case the complex of individuals is sharply distinguished from its related

natural selection, may be explained the transformation of one species into another (*i.e.* the mutations of Waagen), or evolution in time, but not the divergence of one form into two or more, *i.e.* evolution in space, which is due to geographical (space) isolation. But we have already shown that neither can mutations be due to selection.

complex in its morphological structure, it is called a species; if not, a sub-species.

In confirmation of the above-mentioned points, we must refer to the opinion of the well-known palaeobotanist Zeiller (1900): "If species be considered in the wide meaning of the term, if extinct species, whose variations may be traced to their extreme confines, be investigated, it may then be seen that such variations reaching a certain limit cease without crossing the boundary separating them from their most closely allied species. The same is true of genera" (pp. 383-384). If the sequence of genera and species, apparently related and historically succeeding one another, be traced, the series is always an interrupted one, however complete be the palaeontological records: in the end transitional forms are never found (p. 384).

This absence of transitional forms is a consequence of the production of species by means of mutations. Acknowledging progressive evolution, Zeiller supposes that the transformation of forms was accomplished, if not suddenly, at least very rapidly (p. 384).

The notion of the saltatory character of evolution is, in fact, no new one. It has been maintained by many leading naturalists. In spite of the dissimilarity of their opinions, it was entertained by Geoffroy St. Hilaire and Cuvier. Baer in 1876 (p. 436) wrote, "In what form can transmutation be conceived? I answer without hesitation, as a saltatory action; the course of development is subject to certain changes, and in accordance therewith the result is considerably modified."

In general, the principle of Aristotle ("De Incessu Animalium," c. 2 and 8) and Leibnitz, "*natura non facit saltus*" must be admitted with considerable limitations. And perhaps it may be said with equal justice that "natura facit saltus." Every kind of progress is achieved by bounds. *Rhythm*, manifested in the physical as well as in the ideal world, is nothing more than an exhibition of the law of

intermittent development. The birth or death of individuals, species, ideas is a catastrophic process. The manifestation of every class of these phenomena is preceded by a long latent period of development, which follows certain definite laws, and then suddenly culminates in a bound, *saltus*, by which the group emerges into the light, is distributed over the earth's surface, and wins for itself "a place in the sun." The same gradual internal process precedes death, which takes place suddenly. The process of the conversion of gas into liquid is a saltatory modification. The theory of quants, now upheld in physics, teaches that energy emanating from some source is produced not continuously, but issues forth in portions, as it were, in packets or "quants." Not long before the war Henri Poincaré expressed the opinion that the differential calculus, though very convenient as a method, does not truly reflect the processes actually occurring in nature, where quantities tend to approach zero, not by means of infinitely small variations, but in a saltatory, intermittent manner.

Thus, with as much right as Leibnitz, we may bring forward the opposite assertion : natura facit saltus. During certain, sometimes considerable, intervals of time organisms remain in a stationary condition ; a mutational period then sets in, when the production of species is accomplished with particular intensity.

The catastrophic character of the origin of new forms is very well exemplified in palaeontology. The transformation of genera, says Cope (1887, p. 79 ; 1896, p. 25), may have been rapid and abrupt. After an interval of quiet development, at the commencement of many geological periods, we all at once observe a sudden appearance of a number of new groups of organisms. Thus, in the Permian, the Stegocephala suddenly assume their flourishing condition,[1] in the Triassic the reptiles, and in the Lower Cretaceous the angiosperms ; on the limit of the Lower and

[1] They make their first appearance earlier.

Upper Cretaceous the dominant position is held by the teleostean fishes, and in the Lower Tertiary by the Mammalia. Such phases of vigorous production of forms Cope (1868; 1887, p. 112) has called *periods of metamorphosis*, and J. Walther (1908) *anastrophies*.

We shall conclude this section by quoting the following antagonistic opinion expressed by Darwin. "As natural selection acts solely by accumulating slight, successive, favourable variations, it can produce no great or sudden modifications; it can act only by short and slow steps. Hence, the canon of 'Natura non facit saltum,' which every fresh addition to our knowledge tends to confirm, is on this theory intelligible" ("Origin of Species," chap. xv, pp. 413-414). "But I do believe that natural selection will generally act very slowly, only at long intervals of time, and only on a few of the inhabitants of the same region" ("Origin of Species," chap. iv, pp. 84-85). "Why should not Nature take a sudden leap from structure to structure? On the theory of natural selection, we can clearly understand why she should not; for natural selection acts only by taking advantage of slight successive variations; she can never take a great and sudden leap, but must advance by short and sure, though slow steps" ("Origin of Species," chap. vi, p. 156).

On the other hand, Mivart (1871, p. 111) says, "Arguments may yet be advanced in favour of the view that new species have from time to time manifested themselves with suddenness, and by modifications appearing at once, the species remaining stable in the intervals of such modifications."

5. ARE THE LIMITS BETWEEN SPECIES SHARPLY DEFINED?

The conception of the species has been borrowed by naturalists from philosophy. In Aristotle's definition, the species is the essential substance of a thing, "it is an

irreducible peculiarity which makes the thing what it is." By species, says Aristotle, "I mean what any thing actually is and what is its primary entity."

Buffon defined the term species in the following manner: "It is a continuous succession of similar and multiplying beings." "Les espèces," he says, "dans les animaux sont toutes séparées par un intervalle, que la nature ne peut franchir." Such was also the opinion of Kant ("Kritik der reinen Vernunft," 2nd edit., 1787, p. 689): "Species in nature are actually isolated from one another and must, thus, in themselves form a quantum discretum." Among recent authors a similar opinion is held by Bateson (1913), Lotsy (1913, 1916, "Evolution," p. 99), and others.

Darwin, on the contrary, looked upon the term species as one "arbitrarily given, for the sake of convenience, to a set of individuals closely resembling each other; it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms. The term variety, again, in comparison with mere individual differences, is also applied arbitrarily, for convenience sake" ("Origin of Species," chap. ii, p. 42). Similarly, in the opinion of one of the leading systematists in ichthyology, D. S. Jordan (1905, i, p. 293), "the word species is simply a term of convenience, including such members of a group of organisms similar to each other as are tangibly different from others, and are not known to be connected with these by intermediate forms. Such connecting links we may suppose in all cases. We are only sure that they do not now exist in our collections so far as these have been carefully studied."

With regard to this subject we may note that in natural history the conception of the term species has been empirically evolved in the following way. Since a group of individuals resembling each other more than members of any other group has been called a species, it is obvious that in order to ascertain whether we have to deal with a species or not, it is necessary to *compare* it with another group; if after the

comparison it appears that there is a sufficiently perceptible difference between the two, this will then mean that we have to deal with a species; if not, it will appear not to be a species, but some other taxonomic unit. Therefore, those who affirm that a species is something "artificial," an abstraction, invented for its convenience in dealing with specimens in museums, that when a sufficient quantity of material be collected all species may be united into one, and that "nature knows no sub-divisions"—all who think thus fall into a vicious circle: we call species just those very groups which *are distinguished* one from another. And that *in nature* groups of individuals occur of which it can be positively affirmed that they are unconnected with other groups by transitions, is obvious to every naturalist.

Lotsy (1916, "Espèce," p. 106) thus defines a species: in organisms with sexual reproduction a species is "*a complex of all homozygous individuals endowed with a similar* (genetic) *hereditary constitution*" or a similar complex of genes (this latter term, however, Lotsy avoids, preferring to speak of "composition génétique"). This complex represents an elementary species, which is constant (1914, p. 189). Hereditary variability does not exist. Neither the complexes which were called species by Linnaeus, nor the species *of Jordan, nor the pure lines of Johannsen, constitute true* elementary species, for their homozygous character has partly not been demonstrated, and partly does not exist. Therefore Lotsy (1916, p. 108) suggests calling the Linnean complexes *Linneons*, and Jordan's, *Jordanons*. The morphological similarity of its components is typical of the first; and the hereditary transmission of characters when self fertilised or crossed with a similarly constituted individual, is typical of the second. But the "*purity*" *of their hereditary* complexes is not proved in the case of either Linneons or Jordanons. "Pure line" may merely be self-fertilizing organisms, not subsequently segregating during hybridising analysis, nor producing mutations (of de Vries). In the

opinion of Lotsy, both Jordanons and Linneons are obtained by means of the intercrossing of elementary species, *i.e.* of absolutely pure forms.

We have already (Chap. I) stated our objections to the theory of Lotsy. According to this theory there is in fact no evolution, no production of new characters. " Tous les porte-characteres présents dans les organismes supérieurs se trouvaient déjà dans l'ensemble des organismes primitifs " (1914, p. 235). We have shown above, on the contrary, that in the process of geographical differentiation of forms (*i.e.* sub-species) new characters are produced. It is also a plausible suggestion that new characters may originate through the process of mutation (Waagen).

We consider species to be those complexes of *forms* (elementary species, aberrations, morphas, sub-species), and those only, which possess the two following characters: (1) they are *sharply distinguished* morphologically from neighbouring form-complexes; (2) they differ genetically *from neighbouring form-complexes by the possession of a new* character.

In distinction from true or Linnean species (Linneons) with which we have hitherto had to deal, Jordan's species (Jordanons) are the result of a recombination of the same factors; the entire complex of Jordan's species entering into the composition of any Linneon possesses no new character. How the formation of Jordanons is accomplished is very well demonstrated by the observations of Vavilov, which we have mentioned above (Chap. V, § 1). Willis (1922, pp. 216-217) very truly remarks that we cannot regard Jordanons as stages in the evolution of Linneons: " It is clear that the species cannot be composed of many true breeding 'micro-species,' but that the formation of these must be later in the life of a species than the formation of the species itself, and that it is *after* it is formed that a species breaks up into micro-species, not that a species is formed by the accumulation of micro-differences."

Like Jordanons, neither morphas nor aberrations exhibit anything absolutely new. A Linnean species, on the contrary, is always distinguished from another by the presence of something *new*: the same peculiarity is possessed by sub-species, which, however, are *not sharply demarcated* from the maternal forms.

We cannot, therefore, regard the elementary species as a fundamental systematic unit in the way it was recognised by Lotsy (*i.e.* a complex of homozygous individuals with the same set of genes) or by Regel (1913, p. 508)—" The lowest constant systematic unit based upon a separate independent hereditary factor (*hereditary unit, Erbeinheit, gene*), which is determined by means of hybridizing analysis through intercrossing according to Mendel's law." Such elementary species of barleys, wheats, etc., form but subordinate complexes: they interbreed freely and produce offspring which segregate according to Mendel's law and are generally fertile. Linnean species, on the contrary, when crossed *usually*[1] *produce offspring distinguished by their intermediate characters and not segregating*; the fertility of such hybrids is *usually*[1] reduced or absent. In that respect the difference between Jordanons and Linneons is very great. The maternal species and sub-species, on the contrary, so far as we know, in respect of crossing and fertility of hybrids, behave exactly like two distinct Linneons (see above, § 1, p. 366).

The hybrids of crosses between two species *usually* possess an intermediate character. Such are, for instance, the hybrids between the common carp (*Cyprinus carpio*) and the crucian carp (*Carassius carassius*), the bream and the roach, the sterlet and the sturgeon, the horse and the zebra, the bull and the bison, the black cock (*Lyrurus tetrix*) and the capercailzie (*Tetrao urogallus*), the pheasant and the domestic fowl, etc. These hybrids are generally sterile. Sometimes the males alone are sterile, while the females,

[1] We lay especial stress on the fact that we here have to deal with a widely spread phenomenon, subject, however, to exceptions.

when crossed with the male of the initial form, may be fertile (such, for instance, is the case with the European bison (*Bison bonanus*) and the cow). As regards the fertility of hybrids produced from crossing of two species, it sometimes occurs that no segregation ensues and they remain constant, as is the case with crossing of various species of willows. *Some* interspecific hybrids segregate in their progeny according to Mendel's law; such are the hybrids of Antirrhinum investigated by Baur and Lotsy, and those of the pinks (*Dianthus armeria* and *D. deltoides*) studied by Wichler. Lastly, a combination, as it were, of Mendelian inheritance with an intermediate one occurs in certain interspecific hybrids, such as the inheritance in hybrids of various species of the moth Pygaera, described by Federley. In any case, it must be owned that in the crossing of species, when successful, intermediate inheritance and sterility in the first generation is the rule.

If, as is recommended by some, and especially by botanists, the sub-species were to be chosen as the fundamental systematic unit, it would then be defined as a complex of forms, distinguished by the presence of a *new* character. But in that case the character of complexes being sharply demarcated from one another, would be eliminated from the conception of species. And yet in the definition of that conception, the peculiarity of its being isolated must be included.

Two groups of complexes may be distinguished, if the whole range of individuals and forms comprised in each be considered. The first possess something new; they are "nationes," sub-species and species, *i.e.* geographical forms: the second exhibit no new feature; these constitute elementary species, aberrations and morphas; they represent various combinations of dominant and recessive characters.

Forms endowed with an absolutely novel character owe their origin to processes that produce species, *i.e.* to

geographical effects, and, possibly, to geological mutations. Non-geographical forms (morphas, aberrations, elementary species) are, apparently, likewise involved during the *formation of species by the mutational process. At least*, such is the effect of geographical causes: the sub-species produce the same morphas and aberrations as the maternal form (in the Siberian dace the same broad and narrow *morphas occur as are manifested by the maternal form*, *i.e.* the European dace, *Leuciscus leuciscus*). And yet geographical forms (sub-species, "nationes") are subject to variations, as it were, at their own peril and risk.

A very gratifying task for the palaeontologist would be the elucidation of the problem, whether the mutational process (of Waagen) affects the sub-species simultaneously with the initial form.

As mutation always *involves* leaps *or interruptions*, we can understand why species, in our sense of the word, should be sharply distinguished one from another.

Sub-species are always connected with species by means *of transitions, but may in the course of time be disconnected* from them. This may happen in two cases: (1) whenever a sub-species initiates its own cycle of evolution, or (2) when the transitional forms become extinct. The extinction of these latter is not at all an inevitable process, as was *supposed* by Darwin, but is apparently due to accidental causes, as, for instance, to physico-geographical changes within the area occupied by the given transitional form (transgressions of the sea, volcanic eruptions, *glaciations*, *etc.*). *There are no* internal causes which could involve the extinction of transitional forms. We here refer to forms transitional between the species and the sub-species. All other transitional forms (as, for instance, *those which connect the maternal* form with a morpha or aberration) possess no species-forming importance (with respect to species). Lastly, transitional forms obtained by hybridisation have a certain, though restricted, formative importance.

"Varieties are only small species," says Darwin in one of his letters. This is both true and untrue. Under the general term "variety" both geographical and non-geographical forms were formerly confounded. With respect to the former (sub-species and nationes), Darwin's definition is correct; in relation to the latter, it is erroneous.

New species are formed by means either of *divergence* or *substitution.* The first may mean the manner in which sub-species separate from species, although, it should be noted, this "divergence" proceeds in a totally different way from that which was suggested by Darwin; it proceeds, that is to say, by means of transformation *en masse.* By means of substitution, species give rise to other species in the process of mutation (Waagen) by *substituting* a younger species for the maternal one; this is also effected by transformation *en masse.* Both processes have no relation to the struggle for existence, although they give the impression that "there will be a constant tendency in the improved descendants of any one species to supplant and exterminate in each stage of descent their predecessors and their original progenitor" (Darwin, "Origin of Species," chap. iv, p. 93). With equal justice it might be said of the young human generation, as it takes the place of its fathers, that it evinces a tendency to "exterminate its predecessors."

From the definition of the species as given above (see p. 392), it follows, that it is necessary to include in the conception of species all those forms which are connected with the initial complex by means of transitions. In other words, the scope of the species should be extended as far as its natural limits, *i.e.* until it becomes sharply demarcated from neighbouring complexes. Thus, the conception of a species includes the conceptions of morpha, aberration, sub-species (and, of course, of "natio," *i.e.* sub-species of the second order). Such *a species in the wide meaning of the word* we designate by the term *proles,* suggested by Korschinsky (1892). The definition of the species given above is

meant to apply to proles. Species in the restricted sense is a proles without its sub-species, morphas and aberrations. Thus proles = (species + sub-species + natio) + (morpha + aberration)[1].

Had the conception of species with the scope we are now *defining* been *admitted earlier, it would have been easy to* avoid disagreements as to whether species are sharply distinguished one from another or not. Every species in the wide meaning of the word, or proles, is sharply distinguished from *any other proles*; but a species in its *narrow meaning* is, of course, connected by gradual transitions with its subspecies, morphas and aberrations. Thus the proles *Leuciscus cephalis* (chub) is sharply demarcated from the neighbouring proles, as, for instance, from dace, *Leuciscus leuciscus*; but the European chub, *Leuciscus cephalus cephalus* (= species in the narrow meaning of the word) is, of course, not sharply separated from its Caucasian sub-species, *Leuciscus cephalus orientalis.*

When Darwin says that the conception of species does not essentially differ from that of variety, and is implying the *relation of species to sub-species, he is right.* But Darwin's view ceases to be tenable if it be extended so as to apply to the relations of proles to proles: as we have already indicated, chub are sharply distinguished from dace, but the *European chub is not sharply demarcated from* that of the Caucasus.

Finally, we may note that certain proles produce no subspecies; in that case, if non-geographical forms be cast aside, the conception of species coincides with that of proles.

A species (as also a sub-species and a "natio") occupies a definite territory, for the formative act consists in the simultaneous transformation into a new form of a vast number of individuals over a relatively extensive, continuous territory; subsequently the species may become extinct

[1] Proles Korschinsky, 1892 = Formenkreis Kleinschmidt, 1901 = conspecies Bianchi, 1916 = accumulative or polymorphous species R. Regel, 1912.

over a considerable area (a relict species), so that its area may be interspersed among other species ; but in no case does the *species in its distribution blindly follow any neighbouring* species ; only morphas and aberrations are thus subordinated to species.

From the foregoing, as also from the facts stated in Chap. VII, it is clear that the geographical landscape exerts a very powerful influence on the formation of new organic forms. For this reason, following many other systematists (such as Komarov, Semenov-Tian-Shansky, *1910, Bianchi, 1916, and others), I have insisted (1910* ; 1916, pp. xvii-xix) on the importance of a geographical criterion for the determination of species and sub-species : the geographical landscape is one of the nomogenetic factors.

Of course, the action of the geographical landscape is not direct : the environment may create forms through the physiological constitution of the organism. In this case, the words of Goethe are applicable, "Natur hat weder Kern, noch Schale, Alles ist sie mit einem Male." But *the impulses* towards the production of forms may issue both from within and from the environment.

Kusnetzov is right when he says (1920), "Form can be conceived only as a product of an inner physiological activity," for the effect of the geographical landscape is first perceived in the physiological functions of the organism ; and it cannot be conceived otherwise. But I cannot agree with that eminent lepidopterist when, departing from the just premise that "species is a morphological expression, *i.e.* an expression in form of the inner physiological con*ditions of the life of the organism*," he arrives at a conclusion that denies the formative importance of the geographical landscape, and attributes the rôle solely to the agency which we have called autonomic. Yet Kusnetzov himself does not doubt that "the species varies under the influence of the *environment* and of inner causes."[1]

[1] The italics are mine.

We cannot but agree with Kusnetzov that every taxonomic unit, as a species, sub-species or a natio, is, before all, characterised by morphological characters; but morphology itself is a result of both inner (autonomic) and external (geographical) causes. We are bound to acknowledge this where we can clearly and definitely segregate the influence of the geographical landscape (as is the case with species, subspecies, natio).

CONCLUSION

> Of course, in this matter, as elsewhere throughout Nature, we have to do with the operation of fixed and constant natural laws, but *there is, it is believed, already enough evidence to show that these* as yet unknown natural laws or law will never be resolved into the action of "Natural Selection." MIVART, 1871, p. 75.

LET us sum up.

The struggle for life is a fact that cannot be controverted. But it is not connected, as was thought by Darwin, with the selection of single, best adapted individuals. The struggle for existence is not a progressive, it is a conservative agency: it does not spare the most diverging individuals, exterminating the others; but, on the contrary, *maintains the standard and restricts variation* (Ch. I, § 9; Ch. X, § 1). Consequently, *in order to accomplish a change the action of natural selection is not sufficient*; for that, the alteration of the standard is necessary.

Thus it is clear, that evolution does not follow the course of the transmutation of separate individuals, as Darwin believed (for nothing could be achieved thereby: natural selection would, in any case, sweep them away), but operates by means of a transformation of the entire mass, or at least of a considerable number of the individuals subject to change. Evolution bears a sweeping character, and is not due to single, accidentally favourable variations.

We thus reach the problem of the part played by chance.

Even if all the foregoing as to selection were incorrect, even if natural, like artificial, selection could seize upon any accidental favourable variation, still the theory of natural

selection or "selectionism" would be inadequate and generally inadmissible from the point of view of the present doctrine of heredity. And, indeed, selectionism demands that the variability of organisms should be infinite, for, in the opposite case, selection would have *no hold to operate* upon. We know, however, that individual, as also fluctuational (modificational), variability is great (although not infinite), but *possesses no hereditary value*. In this relation, Heincke (1898, p. C1), having for years studied the variability of the herring, very truly said, "Individual variability, however extensive may be its range, is neither a proof of the transformation of species, nor is it a means for such a transformation. It remains and will remain while organisms inhabit the earth, independently of whether species vary or for ever continue the same. It is, in general, a function of life." *Hereditary* variations or mutations (of de Vries) are very rare events, and there can be no question *of their occurring in infinite numbers. Selectionism, or the* theory of accidentally favourable hereditary variations, implies premises that do not exist in nature. On every advocate of selectionism there lies the burden of proving in the first place that the faculty of producing an infinite number of hereditary variations, *i.e.* mutations, is inherent in living beings. But every biologist knows that this cannot be proved: such a suggestion is controverted both by palaeontology and by what we have learnt in our study of heredity.

Moreover, the mutations known hitherto, as we have had occasion to point out, mostly contain something *abnormal*, and cannot thus constitute a basis for the formation of new species.

Darwin repeatedly affirmed that variation subject to selection is individual variation (see section on individual differences in chap. ii of "Origin of Species"). At the same time, he held that this variation is hereditary. But we now know this to be incorrect: fluctuations are not

hereditary. We must therefore admit that selection operates on (de Vries) mutations. These latter, as we have shown, possess no importance in the formation of species.

Another type of variations, to which much attention was given by Darwin, is represented by those which are observed to occur in domestic animals and plants. According to the modern conception of Darwinism, such variations ought to be regarded as mutations. Such, however, is not the case. Mutations by no means occur so frequently among cultivated plants and domesticated animals as was earlier supposed. What were formerly regarded as mutations now appear to be the results of the segregation of the products of crossing between *elementary species (Jordanons), of which a given* Linneon is constituted. At least, mutations of cultivated plants easily fall into the homologous series of Vavilov. Selection can have no evolutionary importance with regard to all these forms : they are all *complete* : we witness merely a regrouping of existing genes, not the formation of new ones.[1]

Baur, who, it must be admitted, acknowledges the selective importance of the struggle for existence, is fully aware of the bearing which the quantity of mutations has on the subject. "The theory of selection," he says (1919, p. 343), "stands or falls, subject to its being ascertained whether mutations are sufficiently frequent and multifarious to accomplish the actual process of selection, or not."

Since the struggle for existence does not lead to the preservation of single favoured individuals, but, on the contrary, tends to maintain the standard, all theories of evolution based on natural selection fall to the ground : to such belong not only the theory of Darwin, but also the mutation theory of de Vries and the hybridisation theory of Lotsy (1914).

That the process of evolution is not ruled by chance may be judged from the very interesting phenomenon of phylo-

[1] On this subject cf. Jennings, 1922, and Goldschmidt, 1923.

genetic acceleration (see Chap. II): characters by which highly organised groups are distinguished appear in the shape of rudiments very much earlier in lowly constituted groups. Hence it may be seen that evolution is to a considerable degree *predetermined*, that it is in the same degree an *unfolding or manifestation of pre-existing rudiments.* Another consequence of the phenomenon of phylogenetic acceleration is as follows: characters occur which owe their development to inner causes, inherent in the very nature of the organism, which we call *autonomic*, independently of any effects from the environment. These autonomic causes are connected with the stereochemical properties of the albumens of the protoplasm of the given organism, which induce the latter to develop in a determined direction. It is obvious that characters, originating through autonomic causes are, as a rule, adaptive.

But in addition to such an unfolding of pre-existing rudiments, the *formation of new characters* takes place; and this is due to the effects of the geographical landscape, which also transfigures the forms in a determined direction. These effects we designate by the name of *choronomic* or geographical.

If we trace palaeontologically the history of several groups of the vegetable or animal kingdom, we shall see that the characters both in phylogeny and ontogeny develop at a different rate: some characters, as it were, recapitulate former stages, others precede (foreshadow) future ones. What had not been fixed in the ontogenic process by some is achieved in the phylogeny of others. Thus, angiosperms accomplish what has been but imperfectly indicated in the Gnetales (as in Welwitschia). The foregoing is but the expression of the idea that development, both individual and phylogenetic, follows certain laws which are common to both. In both cases we encounter *nomogenesis*. Heredity itself, according to our interpretation, loses its enigmatic character: since development follows certain laws, it is

obvious that forms which are the most closely allied in point of *chemical structure (constitution)* (as, for instance, parents and children), are bound to exhibit most resemblance in their morphology.

Accordance with *autonomic laws may best be traced* by studying forms that have developed *convergently*, such as dinosaurs and birds, pterosaurs and birds, Bennettitales and Anthophyta. Compliance with choronomic laws is revealed by investigating the effects of the geographical landscape on organisms.

One of the best proofs of the dependence of evolution upon law, and one of the most convincing refutations of selectionism, is presented by the phenomenon of convergence. By studying this phenomenon more attentively we become persuaded that convergence affects the most essential *features of the structure of the organism, i.e. the skeleton*, the circulatory and nervous systems, etc.; and by that means we are convinced that evolution proceeds in obedience to laws. Darwin represents evolution as a *process of divergence* of characters. As a matter of fact, predominative importance belongs to the *convergence* of characters.

The *evolutionary process should be imagined in the* following manner. A considerable quantity, possibly tens of thousands, of primitive organisms have developed on parallel lines, convergently experiencing approximately the same transformations and effecting that process at various rates, some more rapidly, others more slowly. Thus, mammals consist of several branches, every one of which has independently passed through the (assumed) worm-, fish-, amphibian-, reptile-like stages. The organic world thus develops polyphyletically.

It may be seen from the foregoing that evolution proceeds in accordance with laws, that it is based upon *nomogenesis*. The manifestations of such an accordance with law we know; but why they should be effected in such a manner and not in another is as yet concealed from us. We are equally

ignorant of the causes whereby organisms in general progress in their structure.

Darwin also held that his chance variations were based upon law. Had evolution been in effect Darwin's tychogenesis (from *tyche*, chance), its laws would have been similar to those physical laws which, as is now acknowledged, are of a statistical character; such are the laws of irreversible processes, *e.g.* the conductivity of heat and electricity, diffusion, friction, chemical reactions, which are governed by the second principle of thermodynamics. But in physics accordance with law based upon chance is only reached through the vast, almost immeasurable quantity of molecules which are operated upon by Nature: in one cubic centimetre of air there occurs every second such a number of accidental collisions of molecules of gas, as to be expressed numerically would require a number consisting of 28 ciphers. But in a space containing such a number of molecules which could be numerically expressed in units, physical laws would cease to act: in that case even the second principle of thermodynamics would fail. Had organisms possessed as many hereditary variations as there are accidental collisions between molecules, there then might by chance arise such favourable variations as could be selected by Nature and subsequently fixed. But since no such quantities of mutations are known to exist, the theory of "tychogenesis" has to be abandoned. Nevertheless, the evolution of organisms is nomogenesis, *i.e.* development determined by law. But the nature of these laws is obviously not of a statistical, but of a *dynamic* character, being similar to those which govern reversible processes, such as gravitation, electric and mechanical oscillations, acoustic and electro-magnetic waves.[1]

In conclusion we submit a schematic abstract to show in two parallel columns, how evolution was conceived by

[1] *For distinction between statistical and dynamic laws see Planck, 1914.*

Darwin (*in the first*), *and how it is to be understood on the basis of Nomogenesis* (*in the second*) :—

I	II
1. All organisms have developed from one or a few primary forms, *i.e.* in a mono- or oligo-phyletic manner.	1. Organisms have developed from tens of thousands of primary forms, *i.e.* polyphyletically.
2. Subsequent evolution was divergent,	2. Subsequent evolution was chiefly convergent (partly divergent),
3. based on chance variations,	3. based upon laws,
4. to which single and solitary individuals are subject,	4. affecting a vast number of individuals throughout an extensive territory.
5. by means of slow, scarcely perceptible, continuous variations.	5. by leaps, paroxysms, mutations.
6. Hereditary variations are numerous, and they develop in all directions.	6. Hereditary variations are restricted in number, and they develop in determined direction.
7. The struggle for existence and natural selection are progressive agencies.	7. The struggle for existence and natural selection are not progressive agencies, but being, on the contrary, conservative, maintain the standard.
8. Species arising through divergence are connected by transitions.	8. Species arising through mutations are sharply distinguished one from another.
9. Evolution implies the formation of new characters.	9. Evolution is in a great measure an unfolding of preexisting rudiments.

10. The extinction of organisms is due to external causes, the struggle for existence and the survival of the fittest.

10. The extinction of organisms is due to inner (autonomic) and external (choronomic) causes.

LIST OF LITERATURE CITED

ABEL, O.: Fossile Flugfische. Jahrb. k. k. geol. Reichsanstalt. Wien, Bd. 56, 1906, pp. 1-88.

ABEL, O.: Was verstehen wir unter monophyletischer Abstammung? Verhandl. zool.-bot. Gesell. Wien, LIX, 1909, pp. 243-250; Diskussion, pp. 250-256.

ABEL, O.: Die Vorfahren der Vögel und ihre Lebensweise. Ibidem, LXI, 1911, pp. 144-191.

ABEL, O.: Grundzüge der Paläobiologie der Wirbeltiere. Stuttgart, 1912, pp. xv + 708.

ABEL, O.: Die Stämme der Wirbeltiere. Berlin und Leipzig, 1919, pp. xviii + 914.

ABEL, O.: Lehrbuch der Paläozoologie. Jena, 1920, G. Fischer, pp. xvi + 500.

AGASSIZ, L.: Essay on classification. London, 1859.

ALEKSANDROV, A.: Downward movement of river fry. Petrograd, 1915 (in Russian).

ALEXEIEFF, A.: Comparaison entre la structure des spermatozoïdes et celle des flagellés. Arch. Soc. Russe de Protistologie, II, Moscow, 1923, pp. 295-297.

ANDRUSOV, N.: Fossile und lebende Dreissensidae Eurasiens. Trav. Soc. Natur St.-Pétersb., Géol. et Minér., XXV, 1897, pp. 683 + (resumé) 115.

ANTONIUS, O.: Untersuchungen über den phyletischen Zusammen-hang zwischen Hipparion und Equus. Zeitschr. f. ind. Abstammungslehre, XX, 1919, pp. 273-295.

ARBER, E., *and* PARKIN, J.: On *the origin of angiosperms*. Journ. Linn. Soc., Botany, XXXVIII, 1907, pp. 29-80.

ARISTOTLE: The works of. Vol. IV. Historia animalium. Translated by D'Arcy Thompson. Oxford, 1910.

AUERBACH, E.: Zur Plastizität des Schädels. Archiv für Rassen- und Gesellschaftsbiologie, IX, 1912.

BABCOCK, E., and CLAUSEN, R.: Genetics in relation to agriculture. New York, 1918, pp. xx + 675.

BAER, K. E.: Über Entwickelungsgeschichte der Thiere. Beobachtung und Reflexion. Erster Theil. Königsberg, 1828, 4°, pp. xxiv + 271.

BAER, K. E.: Zum Streit über den Darwinismus. Dorpat, 1873, pp. 15. (Abstract from the Augsburger Allegemeine Zeitung.)

BAER, K. E. v.: Reden gehalten in wissenschaftlichen Versammlungen. Bd. II. Studien aus dem Gebiete der Naturwissenschaften. St. Petersburg, 1876, pp. xxvi + 480.

BAKER, Fr. C.: The Lymnaeidae of North and Middle America, recent and fossil. Chicago Academy of Sciences, Special Publication No. 3, Chicago, 1911, pp. xvi + 539.

BANNERMAN, D. A.: The birds of Gran Canaria. "Ibis" (9), VI, 1912.

BAROULINA, E. J., On vetches (Vicia sativa) weeds in lentils (mimicry in plants). Report of the Third All-Russian Conference on Plant-Breeding, Saratov, 1920.

BARTLETT, H. H.: Mutation en masse. American Naturalist, XLIX, 1915, pp. 129-139.

BATES, H. W.: Contributions to an insect fauna of the Amazon valley. Lepidoptera; Heliconidae, Trans. Linn. Soc., XXIII, 1862, pp. 495-566.

BATES, H. W.: The naturalist on the river Amazon. 4th edition. London, 1876, pp. x + 394, J. Murray.

BATESON, W.: Problems of genetics. New Haven, 1913, Yale Univ. Press.

BATESON, W.: Inaugural address. The Australian meeting of the British Association. Nature, vol. 93, 1914, pp. 635-642.

BAUR, E.: Einführung in die experimentelle Vererbungslehre. 3. und 4. Aufl. Berlin, 1919, pp. xii + 410.

BAUR, G.: The Stegocephali. A phylogenetic study. Anat. Anz., XI, 1896, pp. 657-673.

BEEBE, C. W.: The Tetrapteryx stage in the ancestry of birds. Zoologica, II, No. 2, New York, 1915.

BEKETOV, A.: Plant geography. St. Petersburg, 1896, pp. v + 359 (in Russian).

BELOGOLOVY, J. A.: Segmental position of the skull boundary. Scient. Trans. Moscow Univ., Nat. History, XXVIII, 1911, p. 239 (in Russian).

BERG, L. S.: Die Fische von Turkestan. Mitteil. Turkest. Abteil. Russ. Geogr. Gesell., IV, St. Petersburg, 1905, pp. xvi + 261 (in Russian).

BERG, L. S.: On species and its divisions. *Biologische Zeitschr.*, I, Moscow, 1910 (in Russian).

BERG, L. S.: Note on Perccottus glehni. Annuaire Mus. Zool. Acad. Sci. St. Petersburg, XVII, 1912, pp. i-iii (in Russian).

BERG, L. S.: Poissons (Marsipobranchii et Pisces). Faune de la Russie, (publiée par l'Acad. des Sciences, St.-Pétersbourg), III, livr. 1, 1912, pp. 1-336; livr. 2, 1914, pp. 337-704 (in Russian and Latin).

BERG, L. S.: *Object and scope of geography.* Izv. Russ. Geogr. Obshch. (Bull. Russ. Georg. Soc.), LI, 1915, pp. 463-475 (in Russian).

Berg, L. S.: A specimen of roach with enlarged fins. Vestn. Rybopr. (Bull. of Fisheries). 1916, pp. 616-618 (in Russian).

Berg, L. S.: Les poissons des eaux douces de la Russie. Moscow, 1916, pp. xxvii + 563 (2nd edition 1923) (in Russian).

Berg, L. S.: Sur la distribution du poisson Myoxocephalus quadricornis (L.), fam. Cottidae, et sur quelques problèmes y concernants. Bull. Acad. Sci. St.-Pétersbourg, 1916, pp. 1343-1360 (in Russian).

Berg, L. S.: La distribution bipolaire des organismes et l'époque glaciaire. Bull. Acad. Sci. St.-Pét., XIV (1920), 1923, pp. 273-302 (in Russian).

Berg, L. S.: Theories of evolution. Petrograd, 1922, pp. 120, Academia (in Russian).

Bergson, Henri: L'évolution créatrice. 6 éd. Paris, 1910.

Bernard, Cl.: Leçons sur les phénomènes de la vie communs aux animaux et aux végétaux. Paris, 1878, pp. xxxii + 404.

Berry, E. W.: The geological history of gymnosperms. The Plant World, XIX, 1916, pp. 27-41.

Berry, E. W.: Paleobotany: a sketch of the origin and evolution of floras. Ann. Report Smithson. Inst. for 1918, Wash., 1920, pp. 289-407.

Bianchi, V.: In defence of natural genera. Bull. Acad. Sci., St.-Pétersbourg, 1907, pp. 369-376.

Bianchi, V.: Revision des formes des genres Montifringilla Brehm, *Pyrgilauda* Verr. et *Onychospiza Przw.*, de la *famille des Fringillidae.* Annuaire Mus. Zool. Acad. Sci. Pétersbourg, XII, 1907, pp. 555-597.

Bianchi, V.: Revision des formes de Leucosticte Swains. et Fringillauda Hodgs. de la fam. Fringillidae. Ibidem, XIII, 1908, pp. 28-61.

Bianchi, V.: Oiseaux. Colymbiformes et Procellariiformes. 'Faune *de la Russie,' (publiée par l'Académie des Sciences), Vol. I,* 1913, pp. xxxviii + 979 (in Russian and Latin).

Bianchi, V.: On the species and minor taxonomic unities. Revue Zoologique Russe, I, Moscow, 1916, pp. 294-297.

Boas, Fr.: Changes in bodily form of descendants of immigrants. Washington, 1911, pp. xii + 573. (Reports of the Immigration Commission, vol. 38.) Reprinted: New York, Columbia University Press, 1912.

Boas, J. E. V.: Phylogenie der Wirbeltiere. Die Kultur der Gegenwart. III Teil, IV Abteilung, Bd. IV (Abstammungslehre etc.). Leipzig und Berlin, 1914, pp. 530-605.

Boas, J. E. V.: Die Schläfenüberdachung und das Palatoquadratum in ihrem Verhältnis zum übrigen Schädel bei den Dipnoern und den terrestren Wirbeltieren. Gegenbaur's Morph. Jahrb., Bd. 49, *1915,* pp. 229-307.

Boetticher, H. v.: Untersuchungen über den Zusammenhang zwischen Klima und Körpergrösse der homöothermen Tiere. Zool. Jahrbücher, Abt. Syst., XL, 1915, pp. 1-56.

Boettner, R.: Lithospermum arvense L. filling spring and winter crops. Buli. of Applied Botany, X, Petrograd, 1917, pp. 215-219.

Bogdanov, E. A.: Origin of domesticated animals. Moscow, 1913, pp. vii + 405 (in Russian).

Bolk, L.: Ueber die Körperlänge der Niederländer und deren Zunahme in den letzten Dezennien. Zeitschr. f. Morphologie und Anthropologie, XVIII, 1914, pp. 15-48.

Bower, F. O.: The earliest known land flora. Nature, London, 1920, July, August, p. 681.

Brauer, A.: Die Tiefsee-Fische. II. Anatomischer Teil. Wiss. Ergebn. der Valdivia-Exp., XV, Lief. 2, Jena, 1908, pp. 266, 4°.

Bresciani-Ferroni, C.: Ueber die Korrelation zwischen Körpergrösse und Kopfindex. Archiv für Rassen- und Gesellschafts-Biologie, X, 1913, pp. 452-469.

Broom, R.: On Tritylodon, and on the relationships of the Multituberculata. Proc. Zool. Soc. London, 1910, pp. 760-768.

Broom, R.: On the structure of the skull in cynodont reptiles. Ibidem, 1911, pp. 893-925.

Broom, R.: On the South African pseudosuchian Euparkeria and allied genera. Ibidem, 1913, pp. 619-633.

Bunak, V.: The work of A. D. Elkind on the anthropology, and the present state of the question of the racial type, of Jews. Russ. Anthrop. Journ., XII, No. 1-2, Moscow, 1922, pp. 155-171 (in Russian).

Busch, N.: Plant classification. Petrograd, 1915, pp. 528 (in Russian).

Castle, W.: Is selection or mutation the more important agency in evolution ? The Scientific Monthly, 1916, January, pp. 91-98.

Castle, W.: Genetics and eugenics. 2nd edition. Cambridge, Mass., 1921, pp. viii + 396.

Cholodkovsky, N.: Zur Frage über die Fortpflanzungs- und Entwickelungsweise der viviparen Fliegen. Trav. Soc. Nat. Pétersbourg, XXXVIII, livr. 1, 1907, pp. 106-108.

Cholodkovsky, N.: Ueber den weiblichen *Geschlechtsapparat* einiger viviparen Fliegen. Zool. Anz., XXXIII, 1908, pp. 367-376.

Cholodkovsky, N.: Treatise on entomology. St. Petersburg, 1912, I, pp. xi + 508 ; II, pp. vii + 577 (in Russian).

Clausen, J.: Studies on the collective species Viola tricolor L. II. Botanisk Tidskrift, XXXVI, København, 1922, pp. 363-411.

Cockerell, T. D. A.: The endemic mammals of the British Isles., Amer. Natur., XLVIII, 1914, pp. 177-184. (12 species and 21 sub-species.)

Cope, E. D.: The origin of the fittest. New York, 1887, Appleton, pp. xix + 467.

Cope, E. D.: The primary factors of organic evolution. Chicago, 1896, pp. xvi + 547.

CRAMPTON, G. Ch.: Notes on the ancestry of the Diptera, Hemiptera and other insects related to the Neuroptera. Transactions Entom. Soc. London, 1919, pp. 93-118.

CUÉNOT, L.: Théorie de la préadaptation. Scientia, XVI, 1914, p. 60.

CUÉNOT, L.: La genèse des espèces animales. 2me éd. Paris, 1921, pp. vii + 558.

CUNNINGTON, W. A.: The fauna of the African lakes. Proc. Zool. Soc. London, 1920, pp. 507-622.

DAHL, Fr.: Die Bewegung der fliegenden Fische durch die Luft. Zool. Jahrb., Abt. Syst., V, 1891, pp. 679-688.

DACQUÉ, E.: Paläontologie, Systematik und Deszendenzlehre. In Die Abstammungslehre, Jena, 1991, pp. 169-197.

DANILEVSKY, N. J.: Darwinism. A critical study. St. Petersburg, Vol. I, 1885, pt. 1, pp. xii + 519; pt. 2, pp. xvi + 530 + 148; Vol. II, 1889, pp. 200 (in Russian).

DARWIN, C.: The origin of species by means of natural selection. Sixth edition. London, 1872, J. Murray, pp. xxi + 458.

DARWIN, C.: The variation of animals and plants under domestication. 2 vols. London, 1868, J. Murray, Vol. I, pp. viii + 411; Vol. II, pp. viii + 486.

DARWIN, C.: The descent of man. 2nd edit. London, 1877, J. Murray, pp. xvi + 693.

DARWIN, C.: Life and letters, edited by his son Francis Darwin. 3 vols. London, 1888, J. Murray.

DAVENPORT, C.: The form of evolutionary theory that modern genetical research seems to favour. American Naturalist, L, 1916, pp. 449-465.

DAVIS, BRADLEY MOORE: Genetical studies on Oenothera. III. Further hybrids of Oenothera biennis and O. grandiflora that resemble O. lamarckiana. Amer. Naturalist, XLVI, 1912, pp. 377-427.

DAVIS, B. M.: Oenothera neo-lamarckiana, hybrid of O. franciscana Bartlett × O. biennis. Ibidem, L, 1916.

DELSMAN, H. C.: Der Ursprung der Vertebraten. Mitt. Zool. Station zu Neapel, XX, Berlin, 1913, pp. 647-710.

DEPÉRET, CH.: Les transformations du monde animal. Paris, 1907. (English translation: The transformations of the animal world. London, 1909, Int. Sci. Ser.)

DIENER, K.: Paläontologie und Abstammungslehre. Leipzig, 1910, pp. 140, Sammlung Göschen.

DOFLEIN, F.: Lehrbuch der Protozoenkunde. 4. Aufl., Jena, 1916, pp. xv + 1189.

DOGIEL, V.: Cyclonympha strobila n. gen. n. sp. of Trichonymphidae. Journal de Microbiologie, IV, Petrograd, 1917, pp. 47-56.

DOGIEL, V.: Die Artbilding in der Infusorienfamilie Ophryoscolecidae. Archives Soc. Russe de Protistologie, II, Moscou, 1923, pp. 102-104.

DOGIEL, V.: The transformation of the male pronucleus into a spermatozoon in certain Infusoria during their *conjugation*. Petrograd, 1923, pp. 2-4.

DOGIEL, V.: *Treatise on the comparative anatomy of invertebrates.* I. Integument and skeleton. Petrograd, 1923, pp. 178 (in Russian).

DOLLO, L.: Les lois de l'évolution. Bull. Soc. Belge de Géol., VII, 1893, procès verb., p. 164.

DOLLO, L.: Sur la phylogénie des Dipneustes. Bull. Soc. Belge de Géol., Paléont. et Hydrol., IX, 1895, pp. 79-128, pl. V-X.

DOLLO, L.: Les poissons voiliers. Zool. Jahrb., Abt. Syst., XXVII, 1909, pp. 419-438.

DOROGOSTAISKY, V.: La faune carcinologique du lac Baïkal. Trav. Commiss. pour l'étude du lac Baïkal, I, livr. 2, 1922, pp. 105-153, publ. de l'Acad. Sciences, Petrograd (in Russian).

DRIESCH, H.: Der Vitalismus als Geschichte und Lehre. *Leipzig*, 1905, pp. x + 246, J. Barth.

EIGENMANN, C. H.: Cave vertebrates of America. A study in degenerative evolution. Carnegie Inst. Publ., No. 104, Washington, 1909, pp. ix + 241, 4°.

EIGENMANN, C. H.: The freshwater fishes of British Guiana. Mem. Carnegie Museum, V, Pittsburg, 1912, pp. xxii + 578.

EIMER, THEODOR G. H.: *Die Entstehung der Arten auf Grund von* Vererben erworbener Eigenschaften nach den Gesetzen organi*schen Wachsens.* I. *Jena, G. Fischer, 1888, pp. xii + 461.*

EIMER, TH.: Orthogenesis der Schmetterlinge. Ein Beweis bestimmt gerichteter Entwickelung und Ohnmacht der natürlichen Zuchtwahl bei der Artbildung. Zugleich eine Erwiderung an August Weismann. Leipzig, 1897, pp. x + xvi + 513.

EISENSTÄDTER, J.: Elementargedanke und Übertragungstheorie in der Völkerkunde. Stuttgart, 1912, pp. viii + 206.

EISIG, H.: Über das Vorkommen eines schwimmblasenähnlichen Organs bei Anneliden. Mittheil. Zool. Station zu Neapel, II. 1881, pp. 255-304.

EKMAN, S.: Studien über die marinen Relikte der nordeuropäischen Binnengewässer. Intern. Revue der gesamt. *Hydrobiol.* und Hydrogr., V, 1913, pp. 540-550; VI, 1913-4, pp. 335-371, 493-517; VIII, 1919, pp. 477-528.

ENDERLEIN, G.: Die Landarthropoden der von der Tiefsee-Expedition besuchten antarktischen Inseln. Wiss. Ergebn, der deutschen Tiefsee-Expedition "Valdivia" 1898-99, Bd. III, Lief. 7, Jena, 1903, pp. 199-270.

ENGLER, A.: Syllabus der *Pflanzenfamilien*. 8. Aufl. *Berlin*, 1919.

ESCHERICH, K.: Die Termiten oder weissen Ameisen. Leipzig, 1909, pp. xii + 189, W. Klinkhard. (Compare also *Biol.* Centralbl., 1909, p. 26.)

ETTINGSHAUSEN, C. v.: Zur Theorie der Entwickelung der jetzigen Floren der Erde aus der Tertiärflora. Sitzber. Akad. Wiss. Wien, math.-nat. Cl., CIII, Abth. 1, 1894, pp. 303-392.

FATIO, V.: Faune des vertébrés de la Suisse. Vol. IV. Poissons. Ire partie. Genève et Bâle, 1882, pp. xiv + 786.

FAUSSEK, V.: Recherches biologiques dans la contrée transcaspienne. Mémoires (Zapiski) Soc. Russe Géorg., section de Géogr. génér., XXVII, 1906, p. 193 (in Russian).

FEHLINGER, H.: *Veränderungen der Körperformen bei Nachkommen* der Einwanderer in den Vereinigten Staaten. Peterm. Mitteilungen, 1913.

FILATOFF, D.: The removal and transplantation of the auditory vesicle of the embryo of Bufo. Revue Zoologique Russe, I, Moscou, 1916, pp 48-54.

FISHBERG, M.: The Jews: a study of race and environment. London, 1911, pp. xix + 578.

FLAKSBERGER, C.: Determination of wheats. Bull. of Applied Botany, VIII, Petrograd, 1915, pp. 182-209.

FLAKSBERGER, C.: Triticum compactum auct. Notulae systemat. ex Herb. *Horti Botan.* Petropol., III, 1922, p. 36.

FLAKSBERGER, C.: Determination of true corn-crops. Petrograd, 1923, p. 120 (in Russian; very important).

FRIESE, H., und Wagner, T.: Zoologische Studien an Hummeln. II. Die Hummeln der Arktis, des Hochgebirges und der Steppe. Zool. Jahrb., Suppl. XV, Bd. 1, 1912, pp. 155-210.

FRYER, J. C. F.: *Field observations on the enemies of butterflies in* Ceylon. Proc. Zool. Soc. London, 1911, pp. 613-619.

FRYER, J. C. F.: An investigation by pedigree-breeding into the polymorphism of Papilio polytes. Philos. Trans. R. Soc., ser. B, Vol. 204, 1914, pp. 227-254.

FUNKHAUSER, W.: Biology of the Membracidae of the Cayuga Lake basin. *Cornell University Agric. Exp. Station, Memoir No. 11*, Ithaca, N.Y., 1917, pp. 177-445.

FÜRBRINGER, MAX.: Untersuchungen zur Morphologie und Systematik der Vögel zugleich ein Beitrag zur Anatomie der Stütz- und Bewegungsorgane. II. Allgemeiner Theil. Amsterdam und Jena, 1888, pp. 837-1751, 4° (*especially the Anhang*—Ueber die Abstammung der Vögel aus dem gemeinsamen Stocke der Sauropsiden und ihre Beziehungen zu den Reptilien. Einiges über Kaltblütigkeit und Warmblütigkeit, pp. 1592-1641).

FÜRBRINGER, MAX.: Zur vergleicheinden Anatomie der Brustschulterapparates und der Schultermuskeln. IV Teil. Jenaische Zeitschr. f. Naturwiss., XXXIV, 1900, pp. 215-718.—Idem. V Teil. Ibidem, XXXVI, 1902, pp. 289-736.

FÜRBRINGER, MAX.: Zur Frage der Abstammung der Säugetiere. Denkschr. mediz.-naturw. Gesell. Jena, XI, 1904, pp. 571-604, 4°.

GADOW, H.: Vögel. II. Systematischer Theil. Bronn's Klassen und Ordnungen des Thier-Reichs, Bd. VI, Abth. 4, Leipzig, 1893, pp. vii + 304.

GADOW, H.: Amphibia and Reptiles. Cambridge Nat. History, XIII, London, 1901, pp. xiii + 668.

Gadow, H.: Isotely and Coral-snakes. Zool. Jahrbüch., Abt. Biol., XXI, 1911.

Gates, R.: Mutations and evolution. New Phytologist, XIX, 1920, and separate: London, 1921, p. 118.

Gerschler, M.: Melanismus bei Lepidopteren als Mutation und individuelle Variation. Zeitschr. f. indukt. Abstamm., XIII, 1915, pp. 58-87.

Gaupp, E.: Die Verwandschaftsbeziehungen der Säuger, vom Standpunkte der Schädelmorphologie betrachtet. Verhandl. VIII intern. Zoologen-Kongresses in Graz 1910, Jena, 1912, pp. 215-240.

Gemmill, J.: The teratology of fishes. Glasgow, 1912, pp. xvii + 74, 24 plates, 4°.

Giesenhagen, K.: Anzeichen einer Stammesentwicklung im Entwicklungsgang und Bau der Pflanzen. Die Abstammungslehre. Zwölf Vorträge. Jena, 1911, pp. 291-320.

Goebel, K.: Organographie der Pflanzen. Bd. I, 2. Aufl. Jena, 1913, Fischer, pp. x + 513.

Goetsch, W.: Chimärenbildung bei Coelenteraten. Zool. Anz., LVI, 1923, pp. 289-298.

Goldschmidt, R.: A preliminary report on some genetic experiments concerning evolution. Amer. Naturalist, LII, 1918, pp. 28-50.

Goldschmidt, R.: Einführung in die Vererbungswissenschaft. Leipzig, 1920, pp. xii + 519.

Goldschmidt, R.: Die quantitative Grundlage von Vererbung und Artbildung. Berlin, 1920, Springer, pp. 163.

Goldschmidt, R.: Das Mutationsproblem. Zeitschr. f. ind. Abstamm., XXX, 1923.

Goodrich, E.: On the pelvic girdle and fin of Eusthenopteron. Quart. Journ. Micr. Sci., vol. 45, 1901, pp. 311-324, pl.

Goodrich, E. S.: Cyclostomes and Fishes. In: A treatise on Zoology, by Ray Lankester, part IX, London, 1909, pp. xvi + 518.

Gottschick, F.: Die Umbildung der Süsswasserschnecken des Tertiärbeckens von Steinheim a. A. unter dem Einflusse heisser Quellen. Jenaische Zeitschr. f. Naturwiss., Bd. 56 (N.F. Bd. 49), 1920, pp. 155-216, Taf. x-xii.

Grabau, A.: Studies in Gastropoda. III. Amer. Natur., XLI, 1907, pp. 607-651.

Granger, W.: A revision of the American Eocene horses. Bull. Amer. Mus. Nat. Hist., XXIV, 1907, pp. 221-264.

Gudger, E. W.: Oral gestation in the gaff-topsail catfish, Felichthys felis. Papers from the Depart. Marine Biology of the Carnegie Inst. of Washington, XII, 1918, pp. 25-52.

Guitel, F.: Recherches sur l'anatomie des reins du Cottus gobio. Arch. Zool. expér. et génér., Vol. 52, 1913, pp. 447-471, pl. XX.

Haeckel, E.: Systematische Phylogenie der Wirbelthiere. Berlin, 1895, pp. xx + 660.

HAINES, H.: On two new species of Populus from Darjeeling. Journ. Linn. Soc., Botany, XXXVII, 1906, pp. 407-409.

HANDLIRSCH, A.: Monographie der Phymatiden. Ann. Naturhist. Mus. Wien, XII, 1897, pp. 127-230.

HANDLIRSCH, A.: Die fossilen Insekten und die Phylogenie der rezenten Formen. Leipzig, 1906-08, W. Engelmann, pp. ix + vi + 1430 + xl.

HARRIS, J. ARTHUR.: Supplementary studies on the differential mortality with respect to seed weight in the germination of garden beans. Amer. Naturalist, 1913, pp. 683-700, 739-759.

HARTMANN, E. VON: Philosophie des Unbewussten. 11. Aufl. Leipzig, 1904 (on pp. 333-474 is reprinted the article Wahrheit und Irrthum im Darwinismus, 1874).

HARTMANN, E.: Das Problem des Lebens. Bad Sachsa, 1906, pp. viii + 440.

HAYATA, B.: The natural classification of plants according to the dynamic system. 'Icones Plantarum Formosanarum,' X, pp. 97-334, Taihoku and Tokyo, 1921.

HEINCKE, FR.: Naturgeschichte des Herings. Teil I. Die Lokalformen und die Wanderungen des Herings in den europäischen Meeren. Abhandl. deutsch. Seefisch. Vereins, II, Berlin, 1898, pp. cxxxvi + 138. Tabellen und Tafeln, pp. xi + 223. 26 Taf.

HENNINGER, G.: Die Labyrinthorgane bei Labyrinthfischen. Zool. Jahrb., Abt. f. Anat., XXV, 1908, pp. 251-304.

HENNEGUY, L. F.: Les Insectes. Paris, 1904, Masson, pp. xix + 804.

HERTWIG, O.: Des Werden der Organismen. Eine Widerlegung von Darwins Zufalls-Theorie. Jena, G. Fischer, 1916, pp. xii + 710.

HERTWIG, O.: Allgemeine Biologie. 5. Auflage. Jena, 1920, pp. xvi + 800.

HERTZ, H.: Die Prinzipien der Mechanik in neuem Zusammenhange dargestellt. Leipzig, 1894.

HILZHEIMER, M.: Handbuch der Biologie der Wirbeltiere. Stuttgart, 1913.

HOERNES, R.: Das Aussterben Gattungen und Arten. Verhandl. VIII intern. Zoologen-Kongresses zu Graz 1910, Jena, 1912, pp. 650-664.

HORVATH, G.: Les Polycténides et leur adaptation à la vie parasitaire. Ier Congrès internat. d'entomologie. Bruxelles, 1911, pp. 249-256, pl. XVIII.

HUENE, FR. VON: Die Dinosaurier der europäischen Triasformation mit Berücksichtigung der aussereuropäischen Vorkommnisse. Geolog. und paläont. Abhandl., herausgeg. von E. Koken. Suppl. Bd. I, Jena, 1907-08, pp. xii + 419; 111 plates.

HUENE, FR. VON: Beiträge zur Geschichte der Archosaurier. Geol. und paläont. Abhandl., N.F. XIII, Heft 1, Jena, 1914, pp. 3-52; 7 plates.

HUXLEY, T. H.: Darwiniana. Essays. London, 1907, Macmillan, pp. x + 475.

ISSAJEW, W.: Vererbungsstudien an tierischen Chimären. Biol. Zentralblatt, XLIII, 1923, pp. 115-123.

IVANOV, N. N.: Researches on transformation of azotates in yeast. Journ. Petrograd Agron. Inst., No. 1, 1919, pp. 1-179 (in Russian).

IVANOV, N. N.: On the nature of the proteolytic enzyme of yeast. Biochemical Journ., XII, Cambridge, 1918, pp. 106-119.

IVANOV, S. L.: Regularities concerning the distribution of the reserve oil in the vegetable kingdom. Publications of the Bureau of Plant Breeding, Petrograd, IV, No. 1, 1917, pp. 15-35 (in Russian).

JACOBI, A.: Mimikry und verwandte Erscheinungen. Braunschweig, F. Vieweg, 1913, pp. ix + 216.

JAEKEL, O.: Ueber verschiedene Wege phylogenetischer Entwickelung. Jena, 1902, pp. 60. (Reprinted from Verhandl. V Int. *Zoologen-Congresses zu Berlin*, 1901.)

JENNINGS, H. S.: Behaviour of the lower organisms. Columbia Univ. Biol. Ser., X. New York, 1906, pp. xiv + 366.

JENNINGS, H. S.: Experimental evidence on the effectiveness of selection. Amer. Naturalist, XLIV, 1910, pp. 136-145.

JENNINGS, H. S.: Hereditary characters in relation to evolution. Nature (London), 1917, Vol. 100, pp. 196-198, 213-216.

JENNINGS, H. S.: Variation in uniparental reproduction. Amer. Natur., LVI, 1922, pp. 5-15.

JOHANNSEN, W.: Elemente der exakten Erblichkeitslehre. 2. Aufl. Jena, 1913.

JOHANNSEN, W.: Hundert Jahre Vererbungsforschung. Verhandl. Gesell. deutsch. Naturf. und Aerzte, LXXXVII, Leipzig, 1922.

JOHNSON, R. H.: The Malthusian principle and natural selection. American Naturalist, XLIV, 1912, pp. 372-376.

JORDAN, D. S.: A guide to the study of fishes. New York, I, 1905, pp. xxvi + 624.

JORDAN, D., and EVERMANN, B.: Fishes of North and Middle America. II, Washington, 1898.

JORDAN, D., and SNYDER, J.: A review of the apodal fishes of Japan. Proc. U.S. Nat. Mus., XXIII, 1901.

JOURDAIN, F. C.: Notes on the ornithology of Corsica. Ibis (9), V, 1911; VI, 1912.

KANT, I.: *Kritik der Urteilskraft*. 1790.

KATHARINER, L.: Ueber den Verdauungscanal und die "Wirbelzähne" von Dasypeltis scabra Wagler. Zool. Jahrbüch., Abt. Anat., XI, 1898, pp. 501-158.

KAUFMANN, A.: Theorie und Methoden der Statistik. (Translated from Russian.)

KEELER, CH. A.: Evolution of the colors of North American land birds. Occasional papers of the California Academy of Sciences, III, San Francisco, 1893, pp. xii + 361.

Keibel, Fr.: Das biogenetische Grundgesetz und die Cenogenese. Ergebnisse der Anatomie und Entwickelungsgeschichte, VII, (1897), Wiesbaden, 1898, pp. 722-792.

Keith, A.: The antiquity of man. London, 1916, pp. xx + 519.

Kessler, K. T.: Law of mutual aid. Trav. Soc. Natur. Pétersbourg, XI, livr. 1, 1880, pp. 124-136 (*in Russian*).

Khokhlov, B. P.: *Investigation on the length of the proboscis in* worker bees. Pchelovodnoye Khozyaystvo (Apiculture), No. 2, Moscow, 1916, pp. 16-41 (in Russian).

Kingsley, J. S., and Ruddick, W. H.: The ossicula auditus and mammalian ancestry. American Naturalist, XXXIII, 1899, pp. 219-230.

Klaatsch, H.: Herkunft und Entwicklung des Menschengeschlechts. Weltall und Menschheit, II.

Klaatsch, H.: Kraniomorphologie und Kraniotrigonometrie. Archiv für Anthropologie, N.F., VIII, 1909, pp. 101-123.

Klebs, G.: Willkürliche Entwicklungsänderungen bei Pflanzen. Jena, 1903.

Koken, E.: Die Vorwelt und ihre Entwickelungsgeschichte. Leipzig, 1893, pp. vii + 655 (Schlusskapitel, pp. 616-636).

Koken, E.: Paläontologie und Descendenzlehre. Jena, 1902, pp. 33, G. Fischer.

Koldaev, B. M.: Physiological adaptability of the enteric canal to *the kind of food. 'Priroda' (Nature), Moscow, 1916, pp.*1024-1037 (in Russian).

Komarov, V. L.: Flora Manshuriae. Vol. I. Acta Horti Petropolitani, XX, 1901, p. 559; Vol. III. Ibidem, XXV, 1907, p. 853.

Korschinsky, S.: Plants of Eastern Russia in Europe. Izv. (Bull.) Tomsk. Univ., 1892, *p.* 227 (*in Russian*).

Korschinsky, S.: Heterogenesis and evolution. Bull. Acad. Sci. Pétersbourg, X, 1899, pp. 255-268 (in Russian).

Korschinsky, S.: Heterogenesis und Evolution. Flora, Bd. 89, 1901, Ergänzungsband, pp. 240-363.

Krechetovitch, L. M.: Bisexual cones in Larix. Dnevnik (Proceedings) of the First Congress of Russian *Botanists*, Petrograd, 1921, p. 42 (in Russian).

Kropotkin, P.: Mutual aid. A factor in evolution. London, 1902, W. Heinemann, pp. xix + 348 (Chaps. I and II first published in the Nineteenth Century, 1896, Sept., Novem.).

Kupffer, K. von: Die Morphogenie des Centralnervensystems. In: O. Hertwig, *Handbuch der Entwick. d. Wirbeltiere, Bd.* II, Teil 3, Jena, 1906, pp. 1-272.

Kusnetzov, N. I.: On "taxonomic conceptions" and some attempts to found them on morphological data. Revue Russe d'Entom., XVII (1917), 1921, pp. 79-80.

Kuznetzov, N. I.: Introduction to the classification of the flowering plants. Youryev (Dorpat), 1914, pp. xi + 655 (in Russian).

KUZNETZOV, N. I.: Les principes, les methodes contemporaines et les problèmes futures du système phylogénétique naturel des plantes angiospermes. Bull. Jardin Botan. Russe, XXI, livr. 3, Petrograd, 1922, pp. 16-18.

LAMARCK, J.: Philosophie zoologique. Paris, 1809.

LAUBMANN, A.: Die Vogelwelt der Faeröer. Zool. Jahrb., Abt. Syst., XXXIX, 1915, pp. 55-86.

LINDEN, M. v.: Unabhängige Entwicklungsgleichheit (Homöogenesis) bei Schneckengehäusen. Zeitschr. f. wiss. Zoologie, Bd. 63, 1898, pp. 708-728.

LINDHOLM, W. A.: Die Mollusken des Baikalsees (Gasteropoda et Pelecypoda) systematisch und zoogeographischisch bearbeitet. Kiew und Berlin, 1909, pp. iv + 104. 4°.

LLOYD, R.: What is adaptation? London, 1914, pp. xi + 110, Longmans and Green.

LOEB, JACQUES: The dynamics of living matter. New York, 1906, Columbia University Press.

LOEB, JACQUES: The mechanistic conception of life. Chicago, 1912. (Reprinted from the Popular Science Monthly, 1912, January.)

LOEB, JACQUES: The organism as a whole. New York, 1916.

LOHMANN, H.: Die Gehäuse und Gallertblasen der Appendicularien und ihre Bedeutung für die Erforschung des Lebens im Meer. Verhandl. deutsch. zool. Gesell., XIX, Leipzig, 1909, pp. 200-239.

LOTSY, J. P.: Vorlesungen über Deszendenztheorien mit besonderer Berücksichtigung der botanischen Seite der Frage. 2 Bde. Jena, 1906-08, pp. xii + vi + 799.

LOTSY, J. P.: Vorträge über botanische Stammesgeschichte. Jena, 3 Bde. I. Algen und Pilze. 1907, pp. iv + 828. II. Cormophyta zoidogama. 1909, p. 902. III. Cormophyta siphonogama. I. Teil, 1911, p. 1055.

LOTSY, J. P.: Fortschritte unserer Anschauungen über Deszendenz seit Darwin und der jetzige Standpunkt der Frage. Progressus rei botanicae, IV, Jena, 1913, pp. 361-388.

LOTSY, J. P.: La théorie du croisement. Le croisement non la variabilité est la cause de la formation des espèces. Archives Néerland. des sciences exactes et natur., Série III B, t. II., La Haye 1914, pp. 178-238.

LOTSY, L. P.: Qu'est-ce qu'une espèce? Ibidem, t. III, 1916, pp. 57-110.

LOTSY, J. P.: Evolution by means of hybridization. Hague, 1916, pp. viii + 166, M. Nijhoff.

LOTSY, J. P.: L'Oenothère de Lamarck (Oenothera Lamarckiana de Vries) considerée comme chimère nucléaire. Archives Néerland. des sciences exactes et natur., Série III B, t. III, 1917, pp. 324-350.

LOTSY, J. P.: La quintessence de la théorie du croisement. Ibidem, t. III, 1917, pp. 351-353.

LYDEKKER, R.: A geographical history of mammals. Cambridge, 1896, pp. xii + 400.

MACDOWELL, E. C.: *Piebald rats and multiple factors.* Amer. Naturalist, L, 1916, pp. 719-742.

MACDOWELL, E. C.: Bristle inheritance in Drosophila. I. Extra bristles. Journ. Exper. Zoology, XIX, 1915, pp. 61-98.

MACDOWELL, E. C.: Bristle Inheritance in Drosophila. II. Selection. Journ. Exper. Zool., XXIII, No. 1, 1917, pp. 109-146.

MANDERS, N.: An investigation into the validity of Müllerian and other forms of mimicry, with special reference to the Islands of Bourbon, Mauritius and Ceylon. Proc. Zool. Soc. London, 1911, pp 696-749.

MARTYNOV, A. V.: *Contributions to the Trichoptera fauna of the Caucasus.* Trudy (Transactions) Zool. Labor. Univ. Warsaw, 1912, Warsaw, 1913, pp. 1-111 (in Russian).

MARTYNOV, A. V.: Contributions à la faune des Trichoptères des possessions Russes dans l'Asie centrale. Ann. Mus. Zool., XIX, (1914), 1915. pp 402-437 (in Russian).

MARTYNOV, A. V.: Sur une nouvelle espèce de la tribu des Apataniini et quelques autres formes provenant du pays de Minoussinsk. Ibidem, XXII, 1918, pp. 45-63 (in Russian).

MATTHEW, W. D.: Dinosaurs. New York, 1915, Amer. Mus. Nat. Hist., p. 162.

MÉHELY, L. v.: Die Bedeutung der Epistase in der Artbildung. Verhandl. VIII *intern. Zoologen-Kongresses in Graz 1910*, Jena, 1912, pp. 339-355.

MEILLET, A.: Introduction à l'étude comparative des langues indo-européennes. 3e éd. Paris, 1912, Hachette.

MEISENHEIMER, J.: Geschlecht und Geschlechter im Tierreiche. I. Die natürlichen Beziehungen. Jena, 1921, G. Fischer, pp. xiv + 896.

MENZBIER, M.: Vergleichende Osteologie der Pinguine in Anwendung zur Haupteintheilung der Vögel. Bull. Soc. Natur. Moscou, 1887, No. 2.

METCALF, M.: Adaptation through natural selection and orthogenesis. Amer. Naturalist, 1913, pp. 65-71.

MEYER, K.: Researches on the sporophyte of liverworts of the group of Marchantiales. Moscow, 1916, pp. ii + 185. (From the Scient. Trans. Univ, Moscow, Nat. Hist., XXXIX) (in Russian).

MEYER, K.: Origin of the land flora. Moscow, 1922, pp. 76 (in Russian).

MIDDLETON, A. R.: *Heritable variations and the results of selection in the fission rate of Stylonychia pustulata.* Journ. *experim.* Zoology, XIX, 1915, pp. 451-503.

MICHALSKI, A.: Die Ammoniten der unteren Wolga-Stufe. Mémoires Com. Géol., St.-Pétersbourg, VIII, No. 2, 1890, pp. xi + 330 (Russian) + 331-497 (German), 4°.

MIKHAILOVSKY, N. K.: Notes on Darwinism. 1871. (Works of Mikhailovsky, Vol. I, 1911, pp. 270-300) (in Russian).

MIKHAILOVSKY, N. K.: Natural course of things. 1873. (Ibidem, pp. 300-332) (in Russian).

MILLER, G.: Catalogue of the mammals of Western Europe. L. 1912 (Brit. Mus.).

MIVART, ST. G.: On the genesis of species. New York, 1871, pp. 314.

MOODIE, R. L.: The coal measures Amphibia and Crossopterygia. Amer. Natural., XLIX, 1915, pp. 637-644.

MORGAN, T. H.: Evolution and adaptation. New York, 1903, pp. xiii + 470.

MORGAN, T. H., STURTEVANT, A. H., MULLER, H. J., BRIDGES, C. B.: The mechanism of Mendelian heredity. New York. 1915, H. Holt, pp. xiii + 262.

MOROZOV, G. F.: Forest science. I. Biology of the forest. St. Petersburg, 1912, pp. 83 (in Russian).

NEGER, FR. W.: Biologie der Pflanzen auf experimenteller Grundlage (Bionomie). Stuttgart, 1913, pp. xxix + 775.

NEUMAYR, M.: Zur Kenntniss der Fauna des untersten Lias in den Nordalpen. Abhandl. geolog. Reichsanstalt, VII, No. 5, Wien, 1879, p. 46.

NEUMAYR, M., und PAUL, C. M.: Die Congerien- und Paludinenschichten Slavoniens und deren Faunen. Ein Beitrag zur Descendenz-Theorie. Abhandl. geol. Reichsanstalt, VII, No. 3, Wien, 1875, pp. iv + 113.

NEUMAYR, M.: Die Stämme des Thierreiches. Bd. I. Wien und Prag, 1889, pp. vi + 603.

NOPCSA, FR.: Ideas on the origin of flight. Proc. Zool. Soc., London, 1907, pp. 223-236.

NUSSBAUM, M., KARSTEN, G., WEBER, M.: Lehrbuch der Biologie. Leipzig, 1911.

ORLOV, J. E.: Contingencies and their significance in natural history, Priroda (Nature), Moscow, 1915, pp. 1157-1172 (in Russian).

ORTMANN, A. E.: Grundzüge der marinen Tiergeographie. Jena, 1896, G. Fischer, pp. iv + 96.

ORTMANN, A. E.: On separation, and its bearing on geology and zoogeography. Amer. Journ. Sci. (4), II, 1896.

OSBORN, H. F.: The origin of the Mammalia. American Naturalist, XXXII, 1898, pp. 309-334.

OSBORN, H. F.: Reconsideration of the evidence for a common dinosaur-avian stem in the Permian. American Naturalist, XXXIV, *1900, pp.* 777-799.

OSBORN, H. F.: Origin of the Mammalia. III. Occipital condyles of reptilian tripartite type. Amer. Naturalist, XXXIV, 1900, pp. 943-947.

OSBORN, H. F.: Homoplasy as a law of latent or potential homology. The American Naturalist, XXXVI, Boston, 1902, pp. 259-271. (Reprinted in Evolution, 1907, pp. 228-239.)

OSBORN, H. F.: Evolution of mammalian molar teeth to and from the triangular type. New York, 1907, pp. ix + 250.

OSBORN, H. F.: Darwin and paleontology. Fifty years of Darwinism. New York, 1909, pp. 209-250.

OSBORN, H. F.: *The age of mammals in Europe, Asia and North America.* New York, 1910, Macmillan, pp. xvii + 635.

OSBORN, H. F.: Darwin's theory of evolution by the selection of minor saltations. Amer. Naturalist, XLVI, 1912, pp. 76-82.

OSBORN, H. F.: The continuous origin of certain unit characters as observed by a paleontologist. American Naturalist, XLVI, 1912, pp. 185-206, 249-278.

OSBORN, H. F.: *Tetraplasy, the law of the four inseparable factors of evolution.* Journ. Acad. Nat. Sciences of Philadelphia, (2) XV, 1912, pp. 275-309, 4°.

OSBORN, H. F.: Origin of single characters as observed in fossil and living animals and plants. Amer. Naturalist, XLIX, 1915, pp. 193-239.

OSBORN, H. F.: The origin and evolution of life. London, 1918, G. Bell, pp. xxxi + 322.

OSBORN, H. F.: Men of the Old Stone Age, their environment, life and art. 3rd ed. New York, 1921, pp. xxviii + 559.

PACZOSKI, J. K.: Development of the flora of South-west Russia. Zapiski (Memoirs) Novoross. Obshch. Est., XXXIV, Kherson, 1910, pp. xxxiv + 420 (in Russian).

PACZOSKI, J. K.: Flora of the Kherson-Government. I. Pteridophyta, Gymnosperma, Monocotyledons. Kherson, 1914, pp. lxxx + 548 (in Russian).

PAVLOV, A. P.: Le crétacé inferieur de la Russie et sa faune. Nouv. Mém. Soc. Nat. Moscou, nouv. série, XVI, livr. 3, 1901, p. 87.

PAVLOWSKY, E. N.: Studies in comparative anatomy and embryology of scorpions. Petrograd, 1917, pp. 318 (lithogr.) (in Russian).

PAX, F.: Salicaceae. In: A. ENGLER und K. PRANTL, Die natürlichen Pflanzenfamilien, III Teil, 1. Hälfte. Leipzig, 1894, pp. 29-37.

PEARL, R.: The selection problem. Amer. Naturalist, LI, 1917, pp. 65-91.

PEARSON, K.: The grammar of science. London, 1900, Black, pp. xviii + 548.

PETRONIEVICS, B., and WOODWARD, A. SMITH. On the pectoral and pelvic arches of the British Museum specimen of Archaeopteryx. Proc. Zool. Soc. London, 1917, pp. 1-6, pl. I.

PETRONIEVICS, B.: Comparison between the lower jaws of the cynodont reptiles Gomphognathus and Cynognathus. Proc. Zool. Soc. London (1918), 1919, pp. 197-207.

PIAGET, J.: Notes sur le mimétisme des Mollusques marins littoraux de Binic (Bretagne). Zool. Anz., XLIII, 1913.

PILSBRY, H. A.: Guide to the study of Helices. Manual of Conchology by G. Tryon and H. Pilsbry, IX, Philadelphia, 1894, pp. xlviii + 366.

PISSAREV, V.: De la dégénerescence des froments. Bull. of Applied Botany and Plant-Breeding, XIII (1922-23), *Petrograd*, 1923, pp. 69-70.

PLANCK, M.: Dynamische und statistische Gesetzmässigkeit. Berlin, 1914.

PLATE, L.: Selektionsprinzip und Probleme der Artbildung. Ein Handbuch des Darwinismus. 4. Auflage. Leipzig und Berlin, W. Engelmann, 1913, pp. xv + 650.

PLATE, L.: Vererbungslehre. Leipzig, W. Engelmann, 1913, pp. xii + 519.

PLATE, L.: Prinzipien der Systematik mit besonderer Berücksichtigung des Systems der Tiere. Die Kultur der Gegenwart. *Dritter Teil, 4. Abt., 4. Bd. Abstammungslehre. Leipzig-Berlin*, 1914, pp. 92-164 (list of literature on the question of species).

PLATE, L.: Bemerkungen über die deszendenztheoretische Bewertung der Umwandlungen von Planorbis multiformis. Jenaische Zeitschr. f. Naturwiss., Bd. 56 (N.F. Bd. 49), 1920, pp. 217-224.

POCOCK, R. J.: Palatability of some British insects, with notes on the significance of mimetic resemblances. Proc. Zool. Soc. London, 1911, pp. 809-868.

POPOVA, G.: Wild species of Aegilops and their mass hybridisation with wheat in Turkestan. Bull. of Applied Botany and Plant-Breeding, XIII (1922-23), Petrograd, 1923, pp. 475-482.

PORSCH, OTTO: Wechselbeziehungen zwischen Pflanze und Tier. Die Kultur der Gegenwart, III Teil, IV Abteil., Bd. I, Allg. Biologie. Leipzig und Berlin, 1915, pp. 535-586.

PORTSCHINSKY, J.: Caterpillars and Lepidoptera of the St. Petersburg government. Biological investigations. Horae Soc. Ross., XIX, XXV-XXVII, XXX.

POULTON, E. B.: The value of colour in the struggle for life. Darwin and modern science. Cambridge, 1909, pp. 271-297.

PRAVDIN, I.: Description of some forms of the Russian roach. Contributions to the study of Russian fisheries, IV, fasc. 9, Petrograd, 1915, pp. 91 (in Russian).

PRZIBRAM, H.: Experimental-Zoologie. III. Phylogenese (Artbildung). Leipzig und Wien, 1910, pp. 8 + 315.

PRZIBRAM, H., und BECHER, LEONORE: *Ursachen tierischer Farbkleidung.* I. Vorversuche an Extrakten. Archiv für Entwicklungsmechanik d. Org., Bd. 45, 1919, pp. 83-198.

PRZIBRAM, H.: Ursachen tierischer Farbkleidung. II. Theorie. Ibidem, pp. 199-259.

PUNNETT, R. C.: "Mimicry" in Ceylon butterflies, with a suggestion as to the nature of polymorphism. Spolia Zeylanica, VII, 1911, pp. 1-14.

PUNNETT, R. C.: Mimicry in butterflies. Cambridge, University Press, 1915, pp. viii + 188.

PUNNETT, R. C.: Mendelism. 5th edition. London, 1919, pp. xvi + 319.

RACOVITZA, E. G.: Cirolanides. Arch. Zool. expér. (5), X, 1912.

RAMENSKY, L. G. On the Bergmann-Leuckart law. Journ. Botan. Russe, 1908, No. 5-6 (in Russian).

RANTHER, M.: Ueber den Begriff der Verwandtschaft. Zool. Jahrb., Suppl. Bd. XV. Teil 3, 1912, pp. 69-134.

REES, CH.: The neuromotor apparatus of Paramecium. Amer. Natur., 1921, pp. 464-468.

REGEL, R.: Varieties and races of barleys in Russia. Bull. Bureau für angewandte Botanik, III, St. Petersburg, 1910, pp. 229-257 (in Russian).

REGEL, R.: Die Pflanzenzüchtung vom wissenschaftlichen Standpunkt. Ibidem, V, 1912, pp. 541-623, pl. 88-96.

REGEL, R.: On species formation. Bull. of Applied Botany, X, Petrograd, 1917, pp. 157-181 (in Russian).

RHUMBLER, L.: Ueber die phylogenetisch abfallende Schalen-Ontogenie der Foraminiferen und deren Erklärung. Verhandl. deutsch. Zool. Gesell., VII, Leipzig, 1897, pp. 162-192.

RHUMBLER, L.: Die Foraminiferen (Thalamophoren) der Plankton-Expedition. Zugleich Entwurf eines natürlichen Systems der Foraminiferen auf Grund selektionistischer und mechanisch-physiologischer Facktoren. Ergebn. d. Plankton-Expedition, Bd. III, L. c., Keil und Leipzig, 1919, pp. 1-332 ; 1913, pp. 333-476.

RIPLEY, W. Z.: The races of Europe. A sociological study. London, 1900, pp. xxxii + 624 + x + 160.

RUZICKA, VL.: Ueber Erbsubstanz und Vererbungsmechanik. Zeit. f. allg. Physiologie, X, Jena, 1909, Ref., pp. 1-55.

SAINT-HILAIRE, C.: Untersuchungen über die Placenta der Salpa democratica-mucronata. Arch. f. mikr. Anatomie, Bd. 79, 1912, pp. 59-104, Taf. V-VIII.

SARS, G. O.: Report on the Cumacea of the Caspian Expedition 1904. Trudy (Reports) of the Caspian Exped., IV, St. Petersburg, 1914, pp. 1-32.

SCHACHMATOW, A. A. [Shakhmatov]: Introduction to the study of tho history of the Russian language. Part I. Petrograd, 1916, pp. 146 + iii (in Russian).

SCHEPOTIEFF, ALEX.: Die biochemischen Grundlagen der Evolution. Ergbn. und Fortschritte der Zoologie, Jena, IV, 1913, pp. 285-338.

SCHIMKEWITSCH, W.: Lehrbuch der vergleichenden Anatomie der Wirbeltiere, übersetzt von H. N. Maier und B. W. Sukatschoff. Stuttgart.

SCHIMKEWITSCH, W.: Biological foundations of Zoology. 4th edition. Part I. Petrograd, 1918, pp. vii + 404 (in Russian).

SCHLOSSER, M.: Die fossilen Säugethiere Chinas nebst einer Odontographie der recenten Antilopen. Abhandl. bayer. Akad. wiss., math.-physik. Kl., XXII, München, 1903, pp. 1-221.

SCHMALHAUSEN, J.: Development of the extremities in Amphibia and their bearing on the question of the origin of the extremities of Tetrapoda. Moscow, 1915 (in Russian).

SCHMALHAUSEN, J.: Ueber die Autostylie der Dipnoer und der Tetrapoda. Revue Zool. Russe, III, 1923, pp. 255-262 (also in Anat. Anz., LVI, 1923, pp. 543-550).

SCHMIDT, J.: On the classification of the fresh-water eels (Anguilla). Meddel. Komm. for Havundersög. Fiskeri. IV, No. 7, Köbenhavn, 1914, pp. 1-19.

SCHMIDT, J.: Experimental investigations with Zoarces viviparus L. Comptes Rend. Trav. Labor. Carlsberg, XIV, No. 9. Copenhague, 1920, pp. 14 (Journ. of Genetics, X, Cambridge, 1920, pp. 179-191).

SCHNEIDER, KARL CAMILLO: Einführung in die Deszendenztheorie. 2. Aufl. Jena, 1911, Fischer, pp. xii + 387.

SCHNEIDER, KARL CAMILLO: Zur Theorie des Systems. Zool. Jahrb., Suppl. Bd. XV, Teil 3, 1912, pp. 135-154.

SCHULZE, F. E.: Ueber die Luftsäcke der Vögel. Verhandl. VIII intern. Zoologen-Kongresses in Graz 1910, Jena, 1912, pp. 446-482.

SCOTT, D. H.: The evolution of plants. New York, 1911.

SCOTT, D. H.: The origin of the seed-plants (Spermophyta). Genetica, V, Hague, 1923, pp. 51-60.

SCOTT, W. B.: On variations and mutations. Amer. Journ. of Science (3), XLVIII, 1894, pp. 355-374.

SEELEY, H. G.: Dragons of the air. An account of extinct flying reptiles. London, 1901, Methuen, pp xiii + 239.

SEITZ, A: Allgemeine Biologie der Schmetterlinge. Zool. Jahrbücher, Abt. Syst., V, 1891, pp. 281-343.

SEITZ, A.: Das Fliegen der Fische. Ibidem, pp. 361-372.

SEMENOV [TIAN-SHANSKY], A. P.: On a new genus of Coleoptera Hydrophilidae and its bearing on the question of morphological (morphomatic) parallelism. Horae Soc. Entom. Ross., XXXIV, 1900, pp. 614-630 (in Russian).

SEMENOV TIAN-SHANSKY, A. P.: Die taxonomischen Grenzen der Art und ihrer Unterabteilungen. Berlin, 1910, R. Friedländer, pp. 34, 4°.

SEMENOV TIAN-SHANSKY, A. P.: Beetles of Turkestan. In V. MASALSKI, Turkestan, St. Petersburg, 1913, Devrient, pp. 267-272.

SEMPER, MAX.: Ueber Artenbildung durch pseudospontane Evolution. Centralbl. f. Miner., Geol. und Paläont., 1912, pp. 140-151.

SEWARD, A. C.: Fossil plants. III, Cambridge, pp. xviii + 656; IV, 1919, pp. xvi + 543.

SEWERTZOV, A. N.: Studies in the theory of evolution. Individual development and evolution. Kiev, 1912, pp. v + 300 + ii (in Russian).

SEWERTZOV, A. N.: Modern aims of the theory of evolution. Moscow, 1914, pp. 155 (in Russian).

SEWERTZOV, A. N.: Études sur l'évolution des vertébrés inférieurs. I. Morphologie du squelette et de la musculature de la tête des cyclostomes. Arch. Russes Anat., Hist., Embryol., I, fasc. 1, Petrograd, 1916, pp. 1-114. II. Organisation des ancêtres des vertébrés actuels. Ibidem, fasc. 3, 1917, pp. 425-572.

SHARP, D.: Insects. Cambridge Natural History, V, 1895; VI, 1899 (Russian translation revised and enlarged by N. J. KUSNETZOV, St. Petersburg, 1910).

SHITKOV, B. M.: Age variability and evolution. Moscow, 1922, pp. 70 (in Russian).

SINSKAJA, E.: A contribution to knowledge of regularity (parallelism) in the variability of the family Cruciferae. Bull. Applied Botany, Petrograd, XIII (1922-23), No. 2, pp. 83-89.

SKORIKOV, A. S.: Les bourdons de la faune paléarctique. Partie II, (in the press).

SMITH, ELLIOT: Discussion on the zoological position and affinities of Tarsius. Proc. Zool. Soc. London, 1919, pp. 465-475.

SMITH, F.: A history of Scandinavian fishes. Stockholm, I, 1892, pp. 1-566: II, 1895, pp. 567-1240.

SNODGRASS, R., and HELLER, E. Birds of the Galapagos expedition 1898-99. Proc. Washington Acad. Sci., V, 1904.

SOBOLEW, D.: Skizzen zur Phylogenie der Goniatiten. Warsaw, 1914, pp. 193 (Russian with German summary).

SOLDATOV, V. K.: Studies on the biology of the Salmonidae of the Amur River. Pt. 1. St. Petersburg, 1912, Depart. of Agriculture (in Russian).

SOWINSKI, W. K.: Amphipoden des Baikalsees. Kiev, 1915, pp. iv + 102 + 390 + iii, 4°.

SPEMANN, H.: Zur Entwicklung des Wirbeltierauges. Zool. Jahrb., Abt. Allg. Zool., Bd. 32, 1912, pp. 1-98.

SPEMANN, H.: Zur Geschichte und Kritik des Begriffs der Homologie. Die Kultur der Gegenwart. 3. Teil, 4. Abt., 1. Bd., Allgemeine Biologie. Leipzig und Berlin, 1915, pp. 63-86.

SPEMANN, H.: Die Erzeugung tierischer Chimären durch heteroplastische Transplantationen zwischen Triton cristatus und taeniatus. Arch. f. Entwicklungsmechanik, Bd. 48, 1921, pp. 533-570.

SPENCER, H.: Principles of biology. 2nd edition, 1898 (chapter VIa: Dynamic element in life).

STANDFUSS, M.: Handbuch der Paläarktischen Grossschmetterlinge. 2. Aufl., 1896, pp. xii + 392.

STEINMANN, G.: Die geologischen Grundlagen der Abstammungslehre. Leipzig, 1908, pp. ix + 284.

STEINMANN, G.: Die Abstammungslehre, was sie bieten kann und was sie bietet. Leipzig, 1911, p. 17.

STEPHENSON, J.: Contributions to the morphology, classification, and zoogeography of Indian Oligochaeta. Proc. Zool. Soc. London, 1921, pp. 103-142.

STOCKING, RUTH J.: Variation and inheritance in abnormalities occurring after conjugation in Paramecium caudatum. Journ. experim. Zoology, XIX, 1915, pp. 387-449.

STRAKHOV, N. N.: Darwin. In: Struggle with the Western World in our literature. II. St. Petersburg, 1883, pp. 110-176 (in Russian).

STRAKHOV, N. N.: A complete refutation of Darwinism. Russky Vestnik, 1887, January, pp. 9-62.

STRAKHOV, N. N.: A constant error of Darwinists. Ibidem, 1887, November, pp. 66-114; December, pp. 98-129.

STRAKHOV, N. N.: The debate about the books of N. J. Danilewsky. Ibidem, 1889, December, pp. 186-203.

SUMNER, F. B.: Genetic studies of several goegraphic races of California deer-mice. American Naturalist, XLIX, 1915, pp. 688-701.

SUMNER, F. B.: Geographic variation and Mendelian inheritance in Peromyscus. Journ. Exper. Zool., XXX, No. 3, 1920.

SUSCHKIN, P. P.: *Studies in the morphology of the skeleton of birds.* Comparative osteology of Accipitres and their classification. *Moscow, 1902, pp. iv + 415. (From Zapiski (Scient.* Transactions) of the Moscow Univ., Nat. Hist., XVII) (in Russian).

SUSCHKIN, P. P.: Veränderungen des primordialen Kiefer- und Hyoidapparates *beim Übergang von den Fischen zu den* Tetrapoden. Biologische Zeitschrift, I, Moskau, 1910, pp. 241-258.

SUSCHKIN, P. P.: Is the process of evolution reversible? '*New ideas in biology*,' No. 5, *St. Petersburg, 1915, pp. 1-39 (in* Russian).

SUTULOV, A.: On a species of Polygonum obstructing *flax* crops. (Polygonum linicola mihi.) Izw. (Bulletin) of the Seed Control Station of the Moscow Soc. *of Agric.*, 1 (1914), *fasc.* 2, *Moscow*, 1915, pp. 1-12 (in Russian). (Compare also: A. SUTULOV. Priroda (Nature), Moscow, 1916, pp. 1331-1334, in Russian.)

TERENTJEV, P. V.: On the law of parallel lines in amphibians. Proc. First Congress Russ. Zoologists in *Petrograd 1922. Petrograd*, 1923, pp. 33-35 (in Russian).

THOMPSON, D'A. W.: On growth and form. Cambridge Univ. Press, 1917, pp. xvi + 793.

TSCHERNAVIN, V. V.: Origin of the nuptial dress in salmon. Journ. Petrograd Agron. Inst., No. 3-4, 1921, p. 171 (in Russian).

TSCHERNYSCHEWSKY, N. G.: Origin of the theory of beneficence of the struggle for existence. Russ. Mysl (Russ. Thought), 1888, No. 9 (in Russian).

VAVILOV, N. I.: *Immunity of plants to infectious diseases.* Annales de l'Académie Agronomique Petrovskoé (près Moscou). Année 1918. Moscow, 1918, pp. 242 (with English summary, pp. 221-239).

VAVILOV, N. I.: *The law of homologous series in variation. Journal* of Genetics, XII, Cambridge, 1922, pp. 47-89.

VAVILOV, N. I.: Field crops of South-Eastern Russia. Petrograd, 1922, pp. iv + 228.

VAVILOV, N. I.: A contribution to the classification of soft wheats—Triticum vulgare Vill. Bull. Applied Botany, XIII, No. 1, Petrograd, 1923, pp. 215-257.

VAVILOV, N. I., and KOUZNETZOV, E. S. On the genetic nature of spring and winter varieties of plants. Annals of Agricultural College of Saratov University, 1, Saratov, 1912, pp. 1-22.

VELENOVSKY, J.: Vergleichende Morphologie der Pflanzen. 3 Teile. Prag, 1905-1910, pp. 1211.

VERSLUYS, J.: Streptostylie bei Dinosauriern, nebst Bemerkungen über die Verwandtschaft der Vögel und Dinosaurier. Zool. Jahrbüch., Abt. f. Anat., XXX, 1910, pp. 175-260.

VERSLUYS, J.: Über Streptostylie und ähnliche Zustände bei Sauropsiden. In: Zusammenhang mit Bewegungen im Schädel. *Verhandl. VIII Zoologen-Kongresses in Graz 1910, Jena*, 1912, pp. 490-503.

VIALLETON, L.: Éléments de morphologie des vertébrés. Paris, 1911. O. Doin, pp. xiv + 790.

VRIES, H. DE: Die Mutationstheorie. Leipzig, I, 1901, pp. xii + 648; II, 1903, pp. xiv + 752 (English translation: The mutation theory. London, 1910.)

VRIES, H. DE: Die Mutationen in der Erblichkeitslehre. Berlin, 1912, pp. 42.

VRIES, H. DE: Arten und Varietäten und ihre Entstehung durch Mutation. An der Universität von Kalifornien gehaltene Vorlesungen, übersetzt von H. Klebahn. Berlin, 1906, pp. xii + 530. (English: Species and varieties. Chicago, 1905.)

WAAGEN, W.: Die Formenreihe des Ammonites subradiatus. Geog*nostisch-paläontologische Beiträge, II, München, 1869, pp.* 179-256.

WAGNER, M.: Die Entstehung der Arten durch räumliche Sonderung. Gesammelte Aufsätze herausgeg. von Dr. M. Wagner. Basel, 1889, pp. 667.

WAGNER, W.: L'industrie des Araneina. Mém. Acad. Sci. Pétersbourg (7), XLII, No. 11, 1894, pp. viii + 269, 4°.

WAGNER, W.: Biological foundations of comparative psychology (biopsychology). I. St. Petersburg, without year (1912 ?), pp. viii + 435 + 4 (in Russian).

WALTHER, J.: Geschichte der Erde und des Lebens. Leipzig, 1908.

WARMING, E.: Lehrbuch der oekologischen Pflanzengeographie. 3. Auflage von E. Warming und P. Graebner. Berlin, 1918, Borntraeger, pp. viii + 762 + 64.

WATSON, D. M. S.: The Deinocephalia, an order of mammal-like reptiles. Proc. Zool. Soc. London, 1914, pp. 749-786.

WATSON, D. M. S.: Eunotosaurus africanus Seeley, and the ancestry of the Chelonia. Proc. Zool. Soc. London, 1914, pp. 1011-1020.

WATSON, D. M. S.: A sketch classification of the pre-jurassic tetrapod vertebrates. Proc. Zool. Soc. London, 1917, pp. 167-186.

WATSON, D. M. S.: On Seymouria, the most primitive known reptile. Proc. Zool. Soc. London, 1918, pp. 267-301.

WEBER, M.: Fische der Siboga-Expedition. Leiden, 1913, pp. 710 (Siboga-Expeditie, fasc. LVII).

WEISMANN, A.: The selection theory. 'Darwin and modern science.' Cambridge, 1909, pp. 18-65.

WEISMANN, A.: Vorträge über Deszendenztheorie. 3. Aufl. Jena, 1913. (English translation: The evolution theory, by Thomson. L. Arnold, 2 vols.)

WERTH, E.: Der fossile Mensch. Berlin, 1921.

WETTSTEIN, R.: Grundzüge der geographisch-morphologischen Methode der Pflanzensystematik. Jena, 1898, pp. 64.

WETTSTEIN, R.: Handbuch der systematischen Botanik. 2. Aufl. Wien, 1911.

WHITMAN, C. O.: Orthogenetic evolution in pigeons. Posthumous works, edited by O. Riddle. Carnegie Inst. Washington, No. 257, Vol. I, 1919, pp. x + 194.

WILCKENS, M.: Die Rinderrassen Mittel-Europas. Berlin, 1885, pp. x + 200.

WILCKENS, O.: Stammgarben. Zeitschr. f. ind. Abstamm., XX, 1919, pp. 241-261.

WILLEY, A.: Convergence in evolution. 1911. J. Murray, pp. xv + 177.

WILLIS, J. C.: Studies in the morphology and ecology of the Podostemaceae of Ceylon and India. Annals R. Bot. Gardens, Peradeniya, Vol. I, Colombo, 1902 pp. 267-465.

WILLIS, J. C.: Age and area. A study in geographical distribution and origin of species. Cambridge, 1922, pp. x + 259.

WILLISTON, S. W.: The wing-finger of pterodactyls, with restoration of Nyctosaurus. Journ. of Geology, XIX, 1911, pp. 696-705.

WILLISTON, S. W.: The phylogeny and classification of reptiles. Journal of Geology, XXV, 1917, pp. 411-421.

WITTENBERG, G.: Trematodes of the family Cyclocoeliidae and a new principle of their classification. Trudy (Transactions) State Inst. Exper. Veterinary, Moscow, 1, 1923, p. 61 (in Russian).

WOOD-JONES, F.: Some phases in the reproductive history of the female mole (Talpa europaea). Proc. Zool. Soc. London, 1914, pp. 191-216.

WUNDT, WILH.: System der Philosophie. 3. Auflage. Leipzig, 1907, Bd. I, pp. xviii + 436: Bd. II, pp. vi + 302.

YAKOVLEV, N. N.: Sur la voie de la transformation de genre Chonetes en Productella. Bull. Acad. Sci. de Russie, 1920, pp. 261-266 (in Russian).

Yocom, H.: The neuromotor apparatus of Euplotes patella. Univ. Calif. Publ. Zool., XVIII, 1918, pp. 337-396.

Zawarzin, A. A.: Studies in the histology of the sensory nervous system and optical ganglia of insects. St. Petersburg, 1913, pp. vi + 192 (in Russian).

Zeiller, R.: Éléments de paléobotanique. Paris, 1900, pp. 421.

Zeleny, Ch., and Mattoon, E. W.: The effect of selection upon the "bar eye" mutant of Drosophila. Journ. Exper. Zool., XIX, 1915, pp. 515-529.

Zinger, N. V.: On Spergula and Camelina obstructing flax crops. Travaux Musée Botan. Acad. Sci. St.-Pétersbourg, VI, 1909, pp. 1-303 (in Russian).

Zinger, N. V.: Sub-species of Alectorolophus major . . . and their origin by means of natural selection. Travaux Jardin Botan. de Tiflis, XII, livr. 2, Yourief, 1913, pp. 179-190 (in Russian).

Zittel, K. v.: Grundzüge der Palaöntologie (Paläo-Zoologie). Neubearbeitet von F. Broili, E. Koken, M. Schlosser. Bd. II. Vertebrata. München und Berlin, 1911, pp. vii + 598.

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